ANNALS

OF THE

MISSOURI BOTANICAL GARDEN

Annals
of the
Missouri Botanical Garden

Volume XVIII
1931

With Forty-seven Plates and Twenty-seven Figures

Published quarterly at 8 West King Street, Lancaster, Pa., by the Board of Trustees of the Missouri Botanical Garden, St. Louis, Mo.

Entered as second-class matter at the post-office at Lancaster, Pennsylvania, under the Act of March 3, 1879.

54305

Annals
of the
Missouri Botanical Garden

A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Graduate Laboratory of the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

The Annals of the Missouri Botanical Garden appears four times during the calendar year: February, April, September, and November. Four numbers constitute a volume.

Subscription Price - - - $6.00 per volume
Single Numbers - - - - 1.50 each

Contents of previous issues of the Annals of the Missouri Botanical Garden are listed in the Agricultural Index, published by the H. W. Wilson Co.

LIBRARY
MEDICAL SCHOOL

STAFF
OF THE MISSOURI BOTANICAL GARDEN

Director,
GEORGE T. MOORE.

Assistant to the Director,
KATHERINE H. LEIGH.

HERMANN VON SCHRENK,
Pathologist.

JESSE M. GREENMAN,
Curator of the Herbarium.

ERNEST S. REYNOLDS,
Physiologist.

CARROLL W. DODGE,
Mycologist.

ROLAND V. LA GARDE,
Research Assistant.

ROBERT E. WOODSON, JR.,
Research Assistant.

NELL C. HORNER,
Librarian and Editor of Publications.

BOARD OF TRUSTEES
OF THE MISSOURI BOTANICAL GARDEN

President,
GEORGE C. HITCHCOCK.

Vice-President,
SAMUEL C. DAVIS.

Second Vice-President,
DANIEL K. CATLIN.

L. RAY CARTER.
THOMAS S. MAFFITT.
GEORGE T. MOORE.
ALBERT T. PERKINS.
PHILIP C. SCANLAN.
ETHAN A. H. SHEPLEY.
FRED G. ZEIBIG.

EX-OFFICIO MEMBERS:

GEORGE R. THROOP,
Chancellor of Washington University.

FREDERICK F. JOHNSON,
Bishop of the Diocese of Missouri.

VICTOR J. MILLER,
Mayor of the City of St. Louis.

A. F. SATTERTHWAIT,
President of The Academy of Science of St. Louis.

RICHARD MURPHY
President of the Board of Education of St. Louis.

DANIEL BRECK, *Secretary.*

TABLE OF CONTENTS

		PAGE
The Genus Helicoceras	David H. Linder	1–8
Brief Notes on the Helicosporeae with Descriptions of Four New Species	David H. Linder	9–16
Stimulatory Effects of Radiation from a Quartz Mercury Vapor Arc upon Higher Plants	Harry J. Fuller	17–40
A Study of Plant Distribution in Relation to the Acidity of Various Soils in Missouri	Julian A. Steyermark	41–55
Studies on the Physiology of Plant Disease	Ernest S. Reynolds	57–95
The Genetic Analysis of an Unusual Relationship between Self-Sterility and Self-Fertility in Nicotiana	Edgar Anderson and Dorothea De Winton	97–116
A Monograph of the Genus Sidalcea	Eva M. Fling Roush	117–244
A Revision of the Genus Frasera	Hamilton H. Card	245–282
Notes on the Distribution of Some Rocky Mountain Plants	George J. Goodman	283–286
The Polyporaceae of Colorado	Paul F. Shope	287–456
Alpova, A New Genus of Rhizopogonaceae, with Further Notes on Leucogaster and Arcangeliella	Carroll W. Dodge	457–464
The Chromosome Complements of *Allium stellatum* and *Nothoscordum bivalve*	Edgar Anderson	465–468

PAGE

Hymenomycetous Fungi of Siberia and Eastern Asia, mostly of Wood-Destroying Species.................. Edward Angus Burt 469–487

The Effect of Monochromatic Ultra-Violet Light of Measured Intensities on Behavior of Plant Cells...... Alexander F. Bucholtz 489–508

The Cytology of *Funaria flavicans* Michx. with Special Reference to Fertilization. .... Martha L. Beardsley 509–540

New or Otherwise Noteworthy Apocynaceae of Tropical America........... .... Robert E. Woodson, Jr. 541–556

New South American Asclepiadaceae..... .... Robert E. Woodson, Jr. 557–563

Some Effects of Ultra-Violet Radiation upon the Calcium and Phosphorus Content of Higher Plants................ .... F. Lyle Wynd and Harry J. Fuller 565–572

Studies of the Effects of Different Lengths of Day, with Variations in Temperature, on Vegetative Growth and Reproduction in Cotton................... Earl E. Berkley 573–604

General Index to Volume XVIII.................. 605–612

ERRATA

Plates 1 and 2 should be transposed and the plate numbers changed accordingly.

Page 40, line 9, read "Tomatoes" instead of "Cucumbers"; line 15, read "Cucumbers" instead of "Tomatoes."

Annals
of the
Missouri Botanical Garden

Vol. 18 FEBRUARY, 1931 No. 1

THE GENUS HELICOCERAS

DAVID H. LINDER

Mycologist to the Missouri Botanical Garden
Assistant Professor in the Henry Shaw School of Botany of Washington University

The members of the genus *Helicoceras* were formerly placed in the genus *Gyroceras*. A study of the literature, however, shows that this latter name cannot be applied to the species other than *Gyroceras ammonis*, and for reasons to be shown shortly that name is not valid because of synonymy.

The genus *Gyroceras*, based on *G. ammonis*, was erected by Corda[1] in 1837. His description of the original species runs as follows: "Acervulis atris, confluentibus, stromatis strato inferiore atro; superiore luteo, hyalino, celluloso; floccis infra atris, supra attenuatis luteis; sporis ovalibus discoideis, depressis." It readily can be seen that the presence of a two-layered stroma sharply sets off Corda's species from the non-stromatic ones that make up the remainder of the genus. These latter are parasitic or weakly so, and their vegetative hyphae, although branching, never aggregate to form a stroma under the sporogenous area. A careful examination of the original figure illustrating *G. ammonis* makes it obvious that the present-day conception of the genus is founded on misinterpretation. The "strato superiore" is definitely a layer of short conidiophores beyond which the curved sterile hyphae project. According to Corda, these sterile hyphae break into ovoid discoid spores, a statement that seems partly to have been the cause of the misconception of his genus, and one that needs confirmation before final acceptance. Even though this doubtful point were settled, Corda's genus is not that of later investigators and, in fact, should be relegated to synonymy, as is done in the

[1] Corda, A. C. I., Icon. Fung. **1**: 9. *pl. 2, fig. 141.* 1837.

present paper, and the species placed in the genus *Sarcopodium* of Ehrenburg[1] under the subgenus *Tricholeconium* as it was understood by Lindau.[2]

In 1856, when Montagne and Cesati[3] transferred *Monilia Celtidis* (*Celtis*) to *Gyrocerus*, they established the present conception of the genus. Although they did not give a generic description, they did describe the species rather fully. In the description it is stated that "stroma adest tenuissimum, a Bivona praetermissum, e fibrillis exilissimis materiae grumulosae intermixtus constans, pallidum," and further that the spore filaments "tandem in sporas globosas secedentis." The term stroma is obviously misapplied in this instance, so much so that it would appear that the authors were stretching the term so as to make the species fit into the genus. The statement that the spore filament breaks into globose spores can be substantiated neither by the investigations of *Gyroceras Celtidis* by Killian,[4] nor by the writer's observations on *Helicoceras Oryzae*.

Saccardo[5] in 1886 accepted Montagne and Cesati's interpretation of Corda's genus, and in his generic description perpetuated the erroneous statement that the conidial filament breaks into spores. At the same time he changed the generic name from *Gyrocerus* to *Gyroceras* for etymological reasons and accredited the genus to Corda.

Despite the fact that Saccardo's interpretation of Corda's genus was accepted by Massee,[6] Lindau,[7] and others, according to the rules of nomenclature, when the type species becomes a synonym, the name of the genus also falls into synonymy. The writer therefore proposes the new name *Helicoceras*.

Helicoceras Linder, n. nom.

Gyroceras Corda, Icon. Fung. **1**: 9. *pl. 2, fig. 141.* 1837, of authors, in part.

[1] Ehrenburg, C. G., Silv. Myc. Berol. pp. 12, 23. *fig. 24.* 1818.

[2] Lindau, G. in Rabenhorst, L., Kryptog. Fl. 2nd. ed. **1**(8): 708. 1906.

[3] Montagne and Cesati in Montagne, J. F. C., Syll. Gen. Spec. Cryptogam. p. 308. 1856.

[4] Killian, Ch., Soc. d'Hist. Nat. Afrique Nord, Bull. **60**: 274–281. 1925.

[5] Saccardo, P. A., Syll. Fung. **4**: 266. 1886.

[6] Massee, G., Brit. Fungus Fl. **3**: 365. *fig. 11*, p. 313. 1893.

[7] Lindau, G., in Engler & Prantl, Nat. Pflanzenfam. **1****: 459. *fig. 273a.* 1900; and in Rabenhorst, L., Kryptog. Fl. 2nd ed. **1**(8): 605. 1906.

Mycelia sterilia in substrato extensa, ramosa, septata, non in stromatem aggregata; conidiophoris ex mycelio repente, rectis vel curvis, simplicibus vel ad apices breve-ramosis, apicibus inflatis vel non inflatis; conidiis atris, fuscis, vel subfuscis, multiseptatis, ad septa constrictis, irregulariter curvis, recurvis, vel glomeratis, levibus vel echinulatis.

Sterile mycelium extensive in the substratum, not forming a stromatic layer, branched, septate; conidiophores arising as lateral, erect or ascending branches from the creeping mycelium, simple or terminally short-branched, inflated apically or nearly isodiametric; conidia dilute to deep fuscous, multiseptate, constricted at the septa, irregularly bent, strongly recurved, to two times helically coiled, echinulate or smooth.

The type species is *Helicoceras Celtidis* (Biv.-Bernh.) Linder.

As at present constituted, *Helicoceras* contains four species. Of these, three are parasitic or weakly so. Their economic importance is not great since the hosts attacked are of minor value, with the limited exception of cultivated water-lilies which are occasionally severely damaged by *Helicoceras Nymphaearum*. The four members fall into two equal groups, one characterized by relatively smooth, the other by echinulate, conidia. The resemblance between the two groups is so great, however, that the creation of an additional genus for the two echinulate-spored species would add nothing to the ease of classification of so small a group.

KEY TO THE SPECIES OF HELICOCERAS

1. Conidia smooth, cells shorter than wide; conidiophores not conspicuously inflated nor densely branched at the apices.............................2
1. Conidia echinulate, cells longer than wide; conidiophores mostly inflated at the apex and often densely short-branched.............................3
2. Conidia 5–7.5–(9) μ thick. On *Celtis* spp......................*1. H. Celtidis*
2. Conidia 8–13 μ thick. On *Plantago* spp....................*2. H. Plantaginis*
3. Conidia 60–190 × 5–18 μ. On *Nymphaea* spp..............*3. H. Nymphaearum*
3. Conidia 64–90 × 5.4–9 μ. On seeds of *Oryza*....................*4. H. Oryzae*

1. Helicoceras Celtidis (Biv.-Bernh.) Linder, n. comb.

Monilia Celtidis (*Celtis*) Bivona-Bernhardi, Stirp. Rar. in Sicilia sponte proven. **3**: 18. *pl. 3, fig. 6.* 1813.

Gyroceras Celtidis (Biv.-Bernh.) Mont. & Ces., in Montagne, J. F. C., Syll. Gen. Spec. Cryptogam. p. 308. 1856.

Gyroceras divergens Peck, Torr. Bot. Club Bull. **36**: 155. 1909.

Plate 1, figs. 9–16.

Mycelium light fuscous to fuscous, branched, septate, penetrating through the host tissues. Conidiophores as short branches of the mycelium, simple, little differentiated. Conidia fuscous, curved, circinate, or once-coiled, more conspicuously coiled in dried material, multiseptate, some cells occasionally diagonally or longitudinally septate, constricted at the transverse septa, 50–100 × 5–8 μ, the cells shorter than wide.

Parasitic on leaves of *Celtis* spp., also reported[1] on leaves of *Sponias sinensis*. Europe, North America, and Japan.

Occasionally the outer walls of the spore cells are ruptured and this may give to the spore a false appearance of echinulation. The color of the colonies is fairly constant in all specimens examined. There is, however, in the Sydow Herbarium at Stockholm a form of this species of which the spores are brick-red in color and which is labelled *G. Celtidis* forma *fulvescens*. Excepting for the color of the spores, this material agrees in all details with the typical specimens. *Gyroceras divergens* of Peck is in no way different from the European material.

Specimens examined:

Exsiccati: D. Saccardo, Myc. Ital., 1581; P. A. Saccardo, Myc. Veneta, 276; Kabat & Bubak, Fungi Imp. Exsicc., 395; H. Sydow, Myc. German., 1294; Rabenhorst, Herb. Myc., 275; E. Bartholomew, Fungi Columb., 3525; Seymour & Earle, Econ. Fungi, 147.

United States:

Arkansas: Batesville, *Bartholomew*, in Fungi Columb.

Missouri: Elmwood, *Demetris*, in Kabat & Bubak, Fungi Imp. Exsicc.

Kansas: Manhattan, *Galloway, 1176*, in Seymour & Earle, Econ. Fungi.

Italy: Pedemont, *Cesati*, in Rabenhorst, Herb. Myc. (probably authentic material); Treviso, *P. A. Saccardo*, in Myc. Venet.

Japan: Tokyo, *Shirai*, as *G. Celtidis* forma *fulvescens* (Stockholm).

[1] Lindau, G., in Rabenhorst, L., Kryptog. Fl., 2nd ed. **1**(8): 606. 1906.

2. Helicoceras Plantaginis (Cda.) Linder, n. comb.
Torula plantaginis Corda, Icon. Fung. **3**: 5. *fig. 14.* 1839.
Gyroceras Plantaginis (Cda.) Saccardo, Michelia **1**: 266. 1878.

Plate 1, figs. 17–20.

Mycelium light to deep fuscous, branched, septate, 3–4.5 μ diam. Conidiophores fuscous, as side branches of the vegetative mycelium, occasionally branching terminally (pl. 1, fig. 20), little differentiated. Conidia deep fuscous to almost black, bent or slightly coiled, more pronouncedly coiled in dry material, smooth, simple or branched (pl. 1, fig. 19), multiseptate, constricted at the septa, 50–110 × 7–10 μ, the cells shorter than wide.

On old living leaves of *Plantago* spp. Widespread in Europe.

This species appears to be a weak parasite that only attacks the senescent leaves of the various species of *Plantago.* It is definitely delimited by the host it infects, and the color and size of the conidia.

Specimens examined:

Exsiccati: Wartmann & Schenk, Schweiz. Kryptog., 617; H. Sydow, Myc. German., 1294; Fuckel, Fungi Rhenan., 65.

France: Lorraine near Forbach, *Ludwig,* in Sydow, Myc. German.

Germany: Munchau, in Fuckel, Fungi Rhenan.

Switzerland: Bern, in Wartmann & Schenk, Schweiz. Kryptog.

3. Helicoceras Nymphaearum (Rand) Linder, n. comb.
Helicosporium Nymphaearum Rand, Jour. Agr. Res. **8**: 219–232. *pl. 67–70.* 1917.
Gyroceras Nymphaearum (Rand) Linder, Mo. Bot. Gard. Ann. **16**: 294–295. 1929.

Plate 1, figs. 5–8.

Mycelium intercellular, light brown, often hyaline in culture, septate, and branched. Conidiophores slender, 2–3 μ in diameter, of varying length, inflated at the apices, 6–7.5 μ, often becoming much short-branched apically and thus producing conidia in clusters. Conidia 60–170–(190) × (5)–6.3–14.4–(18) μ, brown, multiseptate, strongly constricted at the septa, the apical cells often subspherical or ovoid, the basal cell rounded-tapering, the

remaining cells longer than wide, minutely echinulate to finely tuberculate.

Parasitic on leaves of *Nymphaea* spp. New York, New Jersey, and Washington, D. C.

In a previous paper (*l. c.*), the writer, through an error, stated that the sclerotia reported by Rand are rounded, subcarbonaceous, and measure 150–190 μ in diameter. The measurements should read 150–900 μ in diameter.

Specimen examined:

United States:

Washington, D. C.: *Rand*, TYPE (U. S. Dept. Agr. and slide in Farlow Herb.).

4. Helicoceras Oryzae Linder & Tullis, n. sp.

Plate 1, figs. 1–4.

Mycelium hyalinum vel albido-fuscum, septatum, ramosum, 1.5–5.4 μ diam.; conidiophoris subhyalinis vel hyalinis, laevibus, simplicibus vel ad apices inflatos breve-ramosis, 1.8–5.4 μ diam., ad extremos 5.4–7.4 μ diam.; conidiis echinulatis, subfuscis, multiseptatis, in septis constrictis, curvatis vel subhelicoideis, in basi et apice rotundatis, 64–90 × 5.4–9 μ.

Vegetative mycelium creeping, hyaline to light fuscous, septate, branched, 1.5–5.4 μ in diameter. Conidiophores subhyaline to hyaline, smooth, simple or short-branched at the inflated apices, of varying length, 1.8–5.4 μ thick, enlarging terminally to 5.4–7.4 μ. Conidia curved or somewhat helically coiled, light fuscous, multiseptate, constricted at the septa, the cells longer than wide, mostly of equal diameter, echinulate, the basal cell abruptly rounded, 64–90 × 5.4–9 μ

On kernels of Chinese rice. Texas.

This species was communicated to the writer by Professor E. C. Tullis, of the University of Arkansas, who isolated it from a kernel of Chinese rice sent to him from Texas. There is no information concerning the pathogenicity of this species.

Superficially, *H. Oryzae* resembles *H. Nymphaearum* and, like that species, also produces small sclerotia on certain media. The conidia when viewed under a hand lens appear either fulvous or fuscous, depending upon their age. The spores of this species are

smaller than are those of the related one, not so deeply constricted at the septa, and the cells are more uniform in size.

Specimen examined:

United States:

Texas: *E. C. Tullis.* TYPE (slides in Mo. Bot. Gard. Herb., the Farlow Herbarium, and the writer's herbarium).

Excluded Species

Gyroceras ammonis Corda, Icon. Fung. **1**: 9. *pl. 2, fig. 141.* 1837. = **Sarcopodium** (Tricholeconium) **ammonis** (Cda.) Linder, n. comb.

Gyroceras saxonicum Lindau, in Rabenhorst, L., Kryptog. Fl., 2nd ed. **1**(8): 606. 1906. = *Coremiella saxonicum* (Lindau) Feurich, Isis Budissina Bautzen **11**: 137. 1928.

Explanation of Plate

PLATE 1

The drawings are made with the aid of a camera lucida. The magnifications in all cases are × 500.

Figs. 1–4. *Helicoceras Oryzae* Linder & Tullis.

In figs. 1 and 2 are shown the typical spores of the species and also variations in the conidiophores. Fig. 4 illustrates a much-branched conidiophore that bears three immature two-celled spores.

Figs. 5–8. *Helicoceras Nymphaearum* (Rand) Linder.

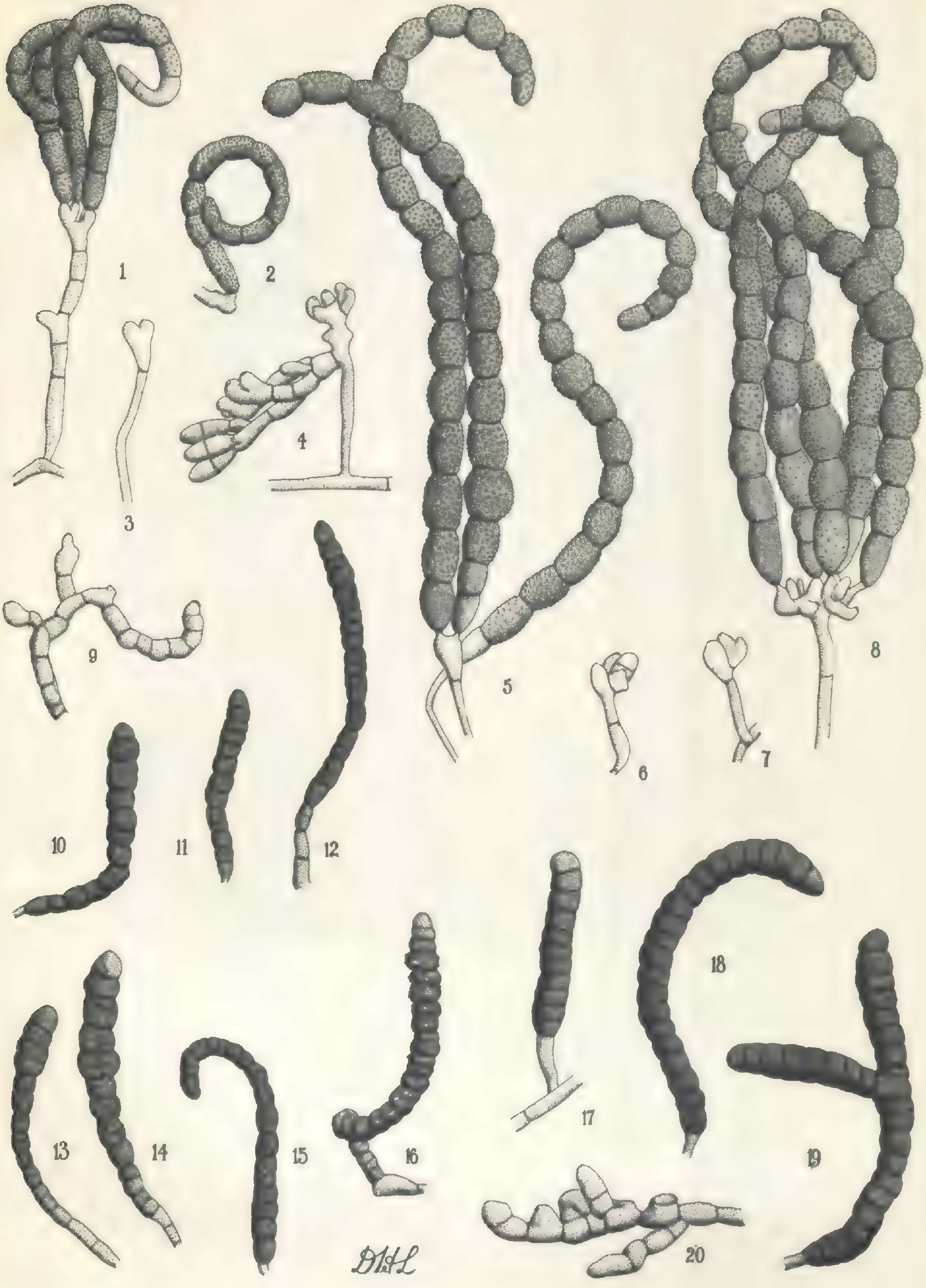
In these figures may be seen the various types of conidiophores, from the simple to the much-branched. The unequal sizes of the cells of the conidia are clearly brought out, as are also the deep constrictions at the septa.

Figs. 9–16. *Helicoceras Celtidis* (Biv.-Bernh.) Linder.

The fulvous form of the species is shown in figs. 9–12. The branched conidiophores shown by fig. 9 are also found in the typical material. In fig. 16, the exospore has ruptured, exposing the lighter-colored endospore.

Figs. 17–20. *Helicoceras Plantaginis* (Corda) Linder.

The simple type of conidiophore may be seen in fig. 17, and a more loosely branched conidiophore in fig. 20. A branched conidium is also depicted in fig. 20. Such branching of conidia is of relatively rare occurrence.



LINDER—HELICOCERAS

BRIEF NOTES ON THE HELICOSPOREAE WITH DESCRIPTIONS OF FOUR NEW SPECIES

DAVID H. LINDER

Mycologist to the Missouri Botanical Garden

Assistant Professor in the Henry Shaw School of Botany of Washington University

Since the publication of "A monograph of the helicosporous Fungi Imperfecti,"[1] the writer has had an opportunity to study additional material of this interesting and beautiful group of Fungi Imperfecti. The material was communicated by Professor G. W. Martin of the University of Iowa and by Mr. John Dearness of Toronto, Canada, and to them the writer wishes to express his sincere thanks. In addition to the material mentioned above, the writer, while examining his collection of Fungi Imperfecti, discovered four additional species: two from the tropics, one from Missouri, and one from Alabama. These are to be described later in this paper.

In addition to the description of the four species, these notes are intended primarily to amplify observations on species which have hitherto been collected only once or twice, and secondarily for the purpose of adding localities and thus enlarging the range of the species as given in the previous paper.[1]

Helicosporium griseum (Bon.) Sacc. This species is reported from North America for the first time and is represented by two collections. The material from Iowa (*T. A. MacBride,* Iowa City, 1909 (Ia.)[2]) agrees very well with the European material. The spore filaments, however, are somewhat thicker (1.4 μ). The Canadian specimen (*Thos. Langton,* Toronto (Ia.)) is almost identical with the Iowan material. It differs only in producing conidia more abundantly and higher on the conidiophores, the latter a character more in agreement with the species as it is delineated by Bonorden[3] in the original figure. The variations between the two collections are very slight and could probably be explained by differences in the environmental conditions.

Helicosporium phragmites v. Höhnel. Although no data were given on the label of this specimen, it appears probable that it was

[1] Linder, D. H. Mo. Bot. Gard. Ann. **16**: 227–388. *pl. 12–31, 17 text figs.* 1929.

[2] The specimens from Professor Martin, deposited in the herbarium of the University of Iowa, are indicated by (Ia) and those from Mr. Dearness by (D).

[3] Bonorden, H. F. Handbuch, p. 74. *fig. 77.* 1851.

collected by MacBride in Iowa (Ia). As is true with the other American collection from Kittery Point, Maine, no perithecial stage was found with the imperfect stage, although it is in close agreement with the European material. The material at hand, as well as that from Kittery Point, strongly suggests an attenuated form of *H. lumbricoides*, but the colonies are not so dense nor are they so readily separable from the substratum. It is interesting to note that this species appears to favor a particular type of substratum,—the Iowan material occurring on old corn stalks, that from Kittery Point on *Carex* stalks, while that from Austria on *Phragmites*.

Helicomyces bellus Morgan. The status of this species becomes very doubtful when material, identified by Morgan, is studied. For example, one specimen (*Morgan*, Ohio, 1902 (Ia)) is clearly *Helicomyces roseus* Lk., while the other (*Morgan*, Ohio?, 1909 (Ia)) is *Helicosporium lumbricopsis* Linder. This latter material can in no manner be considered to belong under *Helicomyces bellus* since Morgan[1] emphasizes the repent character of the hyphae as follows: "The hyphae creep close to the substratum and are nearly concealed by the abundant spores . . . ," and also, "Hyphae creeping, septate, branched, brownish-hyaline, bearing spores on minute lateral teeth." In the material here discussed, the conidiophores are ascending and anastomose after the fashion of *H. lumbricopsis*. Since there is no type material, or at least since it is not available at present, the identity of Morgan's species must remain in doubt.[2]

Helicoma ambiens Morgan. When this species was studied during the preparation of the writer's monograph, only a single specimen was available. Recently two additional collections have been studied, one from Iowa (North Liberty, 1905 (Ia)) and another from Canada (*Dearness*, London, Ontario, 1893 (Ia)), and in both the branching character of the conidiophores and the bluntly rounded, recurved basal end of the conidia proved to be very satisfactory diagnostic characters for the separation of the species from *Helicoma Curtisii*. This latter species is also represented by a collection from Iowa (*T. H. MacBride*, 1889

[1] Morgan, A. P. Cinci. Soc. Nat. Hist. Jour. **15**: 42. *fig. 4.* 1892.
[2] See Note at end of this paper.

(Ia)). The material is at a very advanced stage of development in which the conidiophores have become loosely aggregated to form loose fascicles, within which there are occasional anastomoses between the elements. There is not, however, any evidence of the branching that is so typical of *H. ambiens*.

From Canada an additional station is reported for *Helicoma olivaceum* (Karst.) Linder (*G. K. Bisby*, Winnipeg, May 26 (D)), and for *Helicoon ellipticum* (Pk.) Morgan (*Johnson & Bisby*, Winnipeg, Oct. 25, 1927 (D)). The material is typical of the species represented.

Helicoma repens Morgan. This material, collected and named by Morgan, was recently made available for study for the first time. Since it does not agree entirely with the original description[1] it seems desirable to repeat it and to indicate changes by *italics*.

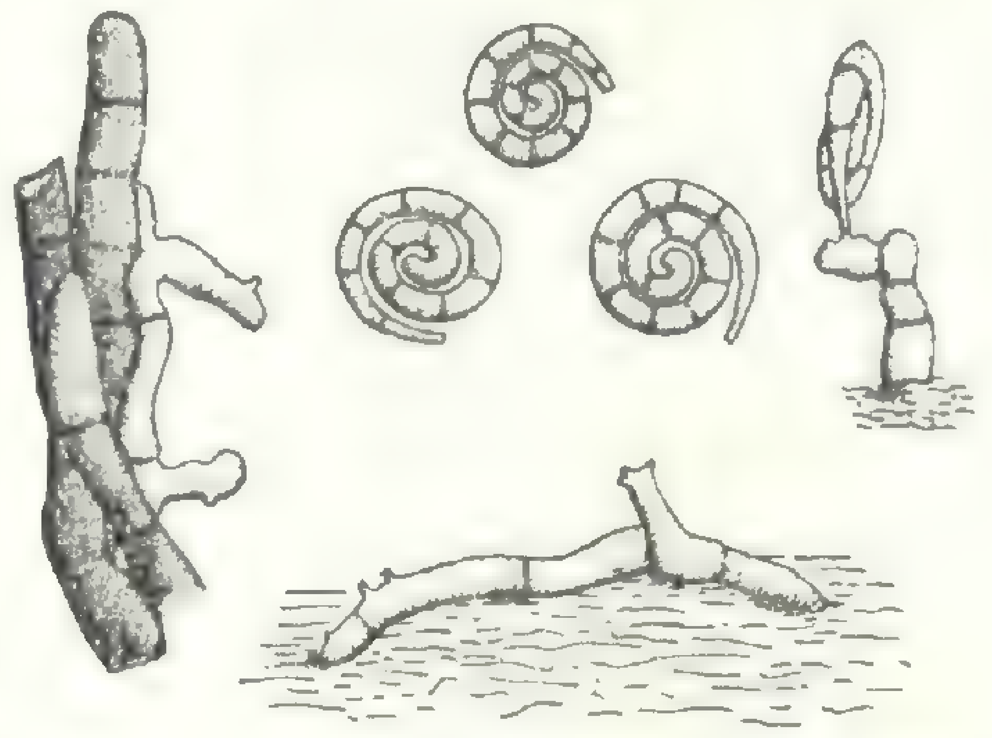


Fig. 1. *Helicoma repens.* × 500.

"Effused, forming a minutely flocculose, pinkish stratum. Hyphae creeping, *or scandent on hyphae of other fungi*, septate, hyaline, with very short ascending branches, which are covered by the abundant spores. Spores hyaline, multiguttulate, *10–16-times septate*, coiled nearly 2½ times; the coil 18–21 (*12–15*) mic. in diameter; the thread 80–100 mic. in length, about 4 (*2–3*) mic. thick; the inner extremity obtuse, the outer (*basal*) long and tapering."

This species closely resembles *Helicoma polysporum*, but is easily separated from it by the more frequently septate spores and the thinner spore filaments. The conidiophores of the two species are much alike. In *H. repens* the conidiophores not only are creeping but, as shown in the accompanying text-figure, are

[1] Morgan, A. P., *l. c.* p. 47. *fig. 12.*

also scandent on the hyphae of other fungi,—in this case on *Helicoma ambiens*.

The specimen studied (*Morgan*, Ohio?, 1887) has been designated as the type, and is deposited in the mycological herbarium of the University of Iowa at Iowa City.

The two following species from the American tropics, one from Missouri, and one from Alabama are described for the first time.

Helicoma Westoni Linder, sp. n.

Plate 2, figs. 1–3.

Mycelia sterilia in substratu immersa; conidiophoris fuscis vel ad apices albido-fuscis, simplicibus, rectis vel curvis, subinde geniculatis, 171–216–(252) μ longis, in basis 7.2–9 μ crassis, in apicibus 5.4–7.2 μ crassis; conidiis acrogenis, subinde pleurogenis, sessilibus, albido-fuscis, in 1½–1¾ spiras convolutis, 11–14-septatis, septis hyalinis; filis conidiorum laeviter fastigatis, basis truncatis, apicibus rotundatis, 11.5–13.5 μ crassis; spiris 33.5–38 μ diam.

Colonies inconspicuous, of scattered conidiophores. Sterile mycelium imbedded in the substratum. Conidiophores fuscous below, dilute or light fuscous at terminal cells, simple, erect or ascending, occasionally geniculate where first spores were produced, 171–216–(252) μ long, 7.2–9 μ thick at base, 5.4–7.2 μ above. Conidia acrogenous, less frequently tardily dehiscent and then pleurogenous, sessile, dilute fuscous, 1½–1¾-times tightly coiled, 11–14-times septate, septa hyaline, filament tapering slightly towards the ends, the basal end truncate, the distal end abruptly rounded, 11.5–13.5 μ thick, the coiled conidia 33.5–38 μ diam.

On decaying sheath of cocoanut palm. Trinidad, B. W. I.

This species is dedicated with great pleasure to Professor William H. Weston, Jr., of Harvard University, as a token of gratitude for the inspiring instruction and the kindly and generous assistance given to the writer while a student.

No species is comparable to this one, since all others with conidia similar to those of *H. Westoni* produce their spores on distinct sporogenous teeth. In this species, the conidia not only

are sessile, but are also provided with a distinct hyaline upward-tapering collar at the base of the spore filament.

Specimen examined:

Trinidad, B. W. I.: St. Augustine, *Linder, 15.* TYPE (in Farlow Herbarium of Harvard University).

Helicoma anastomosans Linder, sp. n.

Plate 2, figs. 4–9.

Coloniae effusae, flocculosae, dilute-roseae; conidiophoris albido-fuscis, pellucidis, simplicibus, rectis vel curvis, parce ramosis vel anastomosis, (20)–30–60–(100) × 3.6–5.5–(6.5) μ; conidiis acrogenis, raro pleurogenis, ad dentes gracilis conspicuos, hyalinis, 18–25-septatis, septis hyalinis, filis in 1½–1¾ spiras convolutis, 3.5–4 μ crassis; spiris 19.8–23.4 μ diam.

Colonies effuse, flocculose, pinkish. Conidiophores dilute fuscous, pellucid, simple, erect or ascending, sparsely branched, anastomosing, (20)–30–60–(100) × 3.6–5.5–(6.5) μ. Conidia acrogenous, less frequently pleurogenous, obliquely attached to conspicuous slender cylindrical sporogenous teeth, hyaline, 18–25-times septate, the septa hyaline; filament 1½–1¾ times coiled, 3.5–4 μ thick, the coiled conidia 19.8–23.4 μ diam.

On decaying manicole palm. British Guiana.

Although resembling *H. Morgani* in its spore characters, this species is quite distinct. The conidiophores, instead of being rather elongate and loosely branching, are short and simple, and anastomose frequently. The sporogenous teeth are prominent and cylindrical. Such characters, although seemingly of minor importance, are remarkably constant and separate this species quite clearly. Still another character is the method in which the conidia are produced. In *H. Morgani*, although two spores may be borne on or near the end of a conidiophore at the same time, they are not as a rule of equal age and hence when both conidia are mature, one, the older, is somewhat lower on the conidiophore than the other. In this species, two or occasionally more conidia are produced almost simultaneously, so that the spores appear frequently in pairs at an equal height on the conidiophore, generally at the apex.

Specimen examined:

British Guiana: Plantation Vryheid, *Linder, 836.* TYPE (in Farlow Herbarium of Harvard University).

Helicoma tenuifilum Linder, sp. n.

Plate 2, figs. 10–13.

Coloniae effusae, "Dark Olive" vel "Chaetura Drab";[1] conidiophoris fuscis vel albido-fuscis, ad cellulas extremas hyalinis, rectis vel curvis, ramosis vel multi-ramosis, perraro anastomosis, 25–60–(80) × 3.6–5 μ; conidiis acrogenis, raro pleurogenis, ad dentes gracilis fastigatos, hyalinis, 18–25-septatis, septis hyalinis, filis in 2¾–3¼ spiras convolutis, 2.5–3.6 μ crassis; spiris 21–28 μ diam.

Colonies effuse, velvety, with age becoming matted, "Dark Olive" to "Chaetura Drab." Conidiophores fuscous to light fuscous below, dilute fuscous to hyaline at the terminal cells, erect or ascending, branched to much branched, very rarely anastomosing, 25–60–(80) × 3.6–5 μ. Conidia acrogenous, less frequently pleurogenous, obliquely attached to short, tapering, sporogenous teeth, hyaline, 18–25-times septate, the septa hyaline; filament 2¾–3¼ times coiled, 2.5–3.6 μ thick, the coiled conidia 21–28 μ diam.

On decaying bark of *Carya?*. Missouri.

With *H. violaceum*, *H. Morgani*, and *H. anastomosans*, *H. tenuifilum* constitutes a rather homogeneous section in the genus *Helicoma*. The four species are characterized by the same type of conidia, and, with the exception of *H. violaceum*, the conidia are attached obliquely to the sporogenous teeth. *H. tenuifilum*, as the name implies, has more slender conidial filaments that are coiled more times. In addition, the conidia are produced singly. The conidiophores also are characteristic in that they are more richly branched, the branches never exceeding the length of the main axis of the conidiophores, as in *H. Morgani*. Occasionally the main axis of the conidiophore elongates (pl. 2, fig. 10) and later becomes much branched on the lower portions, thus resembling a fascicle of conidiophores. Fascicles, however, are not

[1] Ridgway, R. Color standards and nomenclature. Washington, D. C., 1912.

of rare occurrence in the older parts of the colony and give to it its matted appearance. "Sclerotes pedicelées" are present and in some instances suggest perithecia initials.

Specimen examined:

Missouri: Allenton, Oct. 1929, *Linder*, TYPE. (Mo. Bot. Gard. Herb., 68076, and in the writer's herbarium).

Helicomyces fuscopes Linder, sp. n.

Text-fig. 2.

Colonia effusa, stratum tenue, albidum formans; myceliis sterilibus fuscis in substrato immersis vel ad superficiem applicatis; conidiophoris dilute fuscis, rectis, simplicibus vel propter dentes sporigeros conspicuos ad apicem simulate breve ramosis, 1–3-septatis, 18–39–(50) × 2.5–3.6 μ; conidiis hyalinis, acrogenis vel

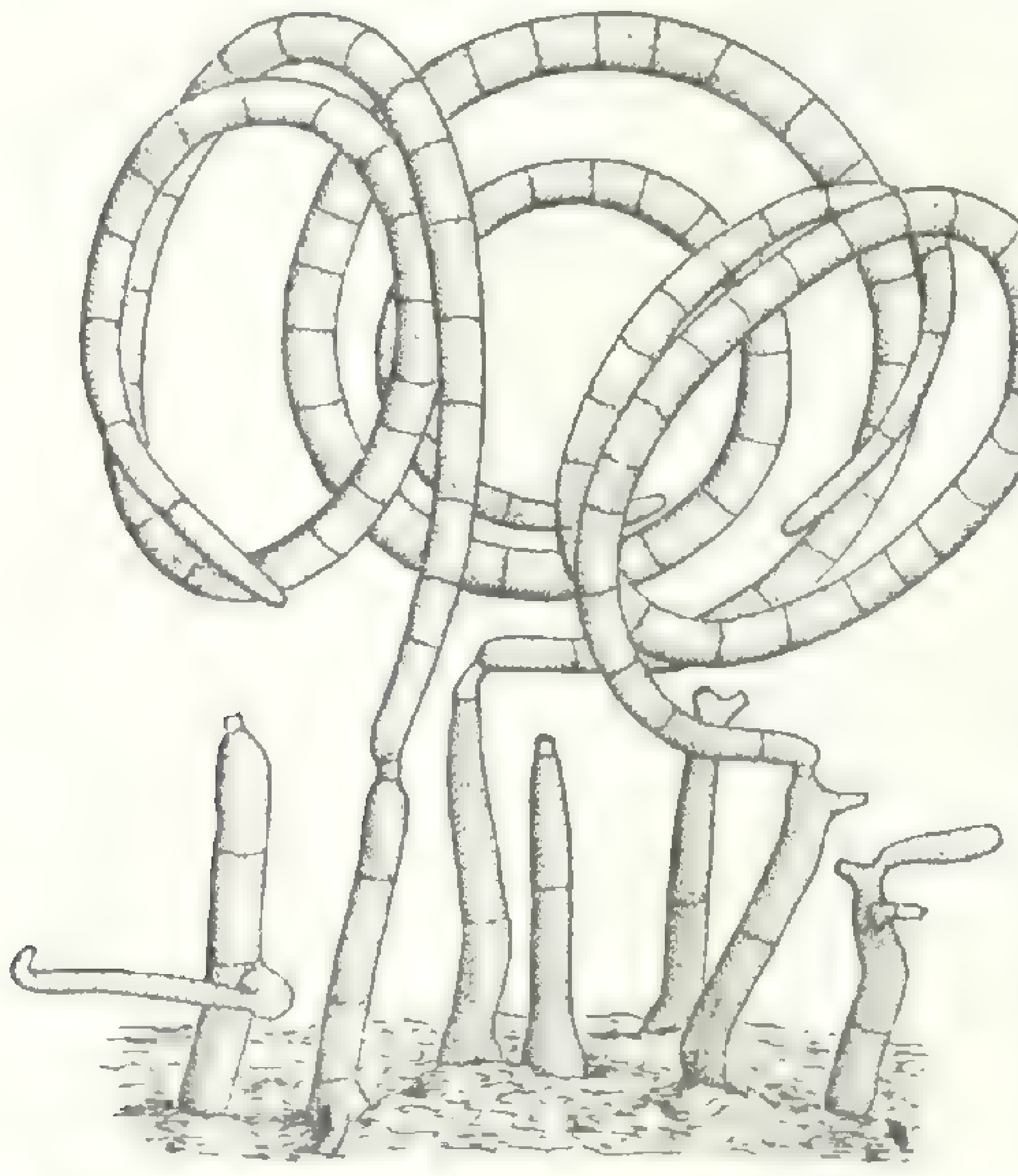


Fig. 2. *Helicomyces fuscopes.* × 500.

aliquando pleurogenis, multiseptatis; filis in spiras 1¼–2¼ convolutis, 3.6–4.5 μ crassis, ad extrema exteriora fastigatis, ad bases rotundatis et oblique complanatis; spiris 39.5–62 μ diam.

Colony effused, forming a thin white flocculose layer. Sterile mycelium immersed in the substratum or closely appressed to the surface, fuscous. Conidiophores dilute fuscous, erect or bent, simple or apparently short-branched above because of the conspicuous sporogenous teeth, 1–3-septate, 18–39–(50) × 2.5–3.6 μ. Conidia hyaline, acrogenous or occasionally pleurogenous, mul-

tiseptate, the filament 1¼–2¼ times coiled, 3.6–4.5 μ thick, tapering toward the acutely rounded distal end, and toward the rounded, obliquely flattened basal end; diameter of coil 39.5–62 μ.

On moist decaying wood. Alabama.

The conidia of this species are attached obliquely, as are those of *H. roseus*, but from that species it may be distinguished by the erect fuscous and somewhat pellucid conidiophores that arise, for the most part, directly from the substratum, and not from hyaline creeping mycelium. The conidia of this species are also somewhat larger than are those of the related species.

Specimen examined:

United States:

Alabama: Montgomery, Oct. 1917, *R. P. Burke, 369.* TYPE. (Mo. Bot. Gard. Herb. 57236).

NOTE.—While this paper was in press, the writer in examining undetermined material, came across a specimen (Montgomery, Alabama, Aug. 1916, *R. P. Burke, 327*) which proves to agree with Morgan's description of the species, especially as regards the repent, anastomosing, fuscous conidiophores. The spore filaments, however, are 1.5–2 μ in diameter, and are coiled only 1½ to 2½ times. For the present, the specimen has been labelled *Helicomyces bellus* Morg.

EXPLANATION OF PLATE

PLATE 2

All drawings are made with the aid of a camera lucida. As reproduced they represent a magnification of × 500.

Figs. 1–3. *Helicoma Westoni* n. sp.

Spores and conidiophores. The characteristic hyaline collars may be discerned at the base of the conidia.

Figs. 4–9. *Helicoma anastomosans* n. sp.

The anastomosing of the conidiophores, typical of the species, is shown in fig. 4, and to a lesser extent in fig. 5. The sporogenous teeth are more prominent in this than in the following species.

Figs. 10–13. *Helicoma tenuifilum* n. sp.

In fig. 10 may be seen an elongated conidiophore that is just beginning to branch below. The sporogenous teeth are short and tapering.

LINDER—HELICOSPOREAE

STIMULATORY EFFECTS OF RADIATION FROM A QUARTZ MERCURY VAPOR ARC UPON HIGHER PLANTS

HARRY J. FULLER

Assistant in Botany, Henry Shaw School of Botany of Washington University

Review of Past Work

The deleterious effects of ultra-violet radiation upon plants have been known since the work of Bailey ('94), who found that electric arc discharges caused the collapse and the loss of color of epidermal cells of *Coleus* plants. Since Bailey many other workers have studied the reactions of plants to ultra-violet radiation, in the majority of cases, that from an unscreened mercury vapor arc or an unscreened iron or carbon arc. Green ('97) found ultra-violet rays destructive to diastase in leaves. Hertel ('05) found a retardation of cyclosis and finally death in leaf cells of *Elodea*, and lethal effects on bacteria and other micro-organisms. Maquenne and Demoussy ('09) showed a killing and blackening effect of ultra-violet rays on plant epidermises. Schulze in the following year, studying the reactions of individual cells to the mercury arc radiation, found disorganization of cytoplasmic and nuclear structures and a repressive effect upon the germination of fungous spores. Stoklasa ('12) carried out lengthy investigations on many types of plants and found only lethal effects. Kluyver ('11) verified the work of Bailey and others and studied in addition the relative effects of ultra-violet rays on various individual organs and tissues of plants; he found the most marked injury in the shorter ultra-violet rays, those below 290 mμ and he failed to discover any resistance on the part of the plant to these rays. Chauchard and Mazoué ('11) found that ultra-violet radiations were destructive to many enzymes in vitro. Bovie ('16), investigating the effects of the Schumann region on both plants and animals, found a marked increase in lethal effects in direct proportion to decreasing wave length. Ursprung and Blum ('17) used deplasmolysis as an indicator of injury and found that the wave-lengths below 290 mμ caused the greatest damage, that the presence of some pigments evidently increases the absorptive

capacity of cells for ultra-violet rays, but that chlorophyllous cells of the epidermis are more resistant than non-chlorophyllous ones.

Burge ('17), working on bacteria that liquefy gelatine, found that the rays injured the organisms not by destroying intracellular enzymes but rather by coagulating the protoplasm. In the next year, Schanz found that plants kept under Euphos glass, which screens out the ultra-violet spectrum, grew more rapidly and flowered earlier than plants which received even very small amounts of ultra-violet. Again Schanz ('19) found the maximum growth of plants in height occurred when the blue-violet portion of the spectrum was removed. Luers and Christoph ('23) studied further the injurious effects of ultra-violet upon yeasts, and in the same year Tanner and Ryder ('23) published results on similar experiments with yeasts; they found that the fermentative ability of the cells decreased in proportion to the length of radiation, that pigmented yeasts are more resistant to ultra-violet than colorless forms, and that there is evidently a relationship between cell size and the effects of radiation, since smaller yeast cells seemed more sensitive to injury than did larger ones. Coblentz and Fulton ('24) found that wave lengths extending from 365 mμ down through the Schumann region were bactericidal, the greater injury occurring in the shorter rays. Brooks ('26) studied the penetration of 2-, 6-dibromophenolindophenol into rayed cells of *Valonia* and found that the penetration of the dye was greater when the shorter waves were employed, which would seem to indicate that protoplasm loses its power of selective absorption under such treatment. Gibbs ('26), studying the effects of radiation from an unscreened mercury arc on *Spirogyra submaxima affinis* and *S. nitida affinis*, found that only rays of less than 3126 Ångstrom units appeared to be toxic. Russell and Russell ('27) rayed seedlings with an unscreened mercury arc and found that dwarfing resulted in direct proportion to the duration of exposure; they also found that the injurious effects were more marked in etiolated than in normal seedlings.

This is by no means all of the work which has been done upon the subject, but it is representative of the various aspects of the problem, and it illustrates all the toxic effects of ultra-violet radiation on plants, which may be summed up as follows:

1. Formative changes in the organism as a whole—e. g., the collapse of epidermal tissue, the burning off of hairs, the blackening of leaves, reduction in size of leaves, general dwarfing of the organism, etc.

2. Structural changes in the protoplasm: coagulation, bursting of cells, clumping of plastids, destruction of vacuoles, etc.

3. Changes in physiological processes: loss of selective absorption, cessation of cyclosis, aberrations of mitosis, destruction of enzymes, etc.

4. As the end result of the above-mentioned changes, the death of the organism.

That accelerative stimulation of plants can be brought about by ultra-violet radiation is another aspect of the subject which has received attention and which has proved extremely controversial in nature, in contrast to the subject of injurious effects. Numerous workers have reported varied types of stimulatory effects on both lower and higher plants—stimulated growth, increased production of food substances, of pigments, stimulated reproductive activity, etc.

Bonnier and Mangin ('86) reported a slight stimulatory effect of ultra-violet upon assimilatory processes in the plant. Tolomey ('94), using a magnesium light as a source of ultra-violet rays, found an increased formation of food substances in rayed plants. Grantz ('98) found that ultra-violet radiation caused an increase in the numbers of fruiting bodies produced by certain fungi. Laurent and Marchal ('03) reported that ultra-violet promoted the synthesis of proteins in plants. Stoklasa ('12) found that *Azotobacter* cultures, when rayed for very short periods—from 1 to 8 seconds—showed increased growth. Tsuji ('18) obtained increased growth and a higher percentage of sugar in sugar cane which was given weak doses of ultra-violet rays. Dufrenoy ('25) rayed zoospores of *Blephorospora* and *Phytophthora* and found that when the period of exposure was reduced to two minutes, the cilia were withdrawn within five minutes preparatory to germination, a process which normally requires several hours; when the dosage of ultra-violet was increased, only injury resulted. Euler ('25) obtained increased growth of the mycelium of *Penicillium glaucum* Link and *Rhizopus chinensis* Saïto by short exposures

to an unscreened arc, and he asserted that there is a certain optimal period of radiation for organisms, above which only injury occurs.

Coward ('27) reported an accelerated formation of vitamin A in the tissues of wheat seedlings under the influence of ultra-violet radiation; he found that this effect occurred only when rays shorter than 3130 Ångstrom units were removed. Sheard and Higgins ('27) found the shorter ultra-violet wave lengths to be stimulatory to the germination of seeds of cucumber and the longer wave lengths effective in promoting later growth of the seedlings. They explain the inhibitory effects of the rays ranging from 270 mμ to 320 mμ as being caused by the action of these rays in coagulating the seed albumen. They also state that the lesser wave-lengths of light, especially those of the near or biologic ultra-violet, act as stimulative agents which modify the endogenous growth of the cells and of the organism, whereas the greater wave lengths of visible and infra-red rays influence the exogenous metabolic processes in the subsequent growth and development of the plant. Beeskow ('27) found that a ½-minute daily irradiation of soy-bean seedlings under an unscreened mercury vapor arc caused no injury and in some cases seemed to produce a slight stimulation to growth. Beeskow further discovered that rayed plants showed a slight increase in calcium and phosphorus content.

Nadson and Philippov ('28) reported that the longer ultra-violet rays stimulated the growth of several yeasts and mucors, while the shorter rays killed the organisms; in some of the fungi with which they worked, they found an increase in the numbers of reproductive organs produced, both asexual and sexual, under the influence of ultra-violet radiation. Stevens ('28) rayed cultures of *Coniothyrium* and *Glomerella* with a mercury vapor arc and found that the numbers of perithecia and pycnidia were greatly increased; in these fungi the reproductive organs are not normally produced until the cultures are very old, but under the influence of the ultra-violet radiation, they appeared almost immediately. This really cannot be considered as accelerative stimulation, since Klebs has shown that in many lower organisms, reproductive processes take place only when environmental con-

ditions become suddenly unfavorable for vegetative growth. The subject is by no means settled, however, and will bear further investigation. Stevens found only lethal effects on spores and mycelium with the unscreened lamp; the rays instrumental in bringing about the production of reproductive organs were those shorter than 313 mμ.

Delf, Ritson and Westbrook ('27), using an unscreened mercury arc, found injurious effects on a variety of plants, but found that when seedlings of some of them were rayed for 30 seconds daily, a small amount of increased growth was obtained; the number of plants used was small, however, and hence the results cannot be considered as of great reliability. McCrea ('28–'29) found that plants of *Digitalis purpurea* which were grown under vita-glass, transmitting to 289 mμ, in a greenhouse through the seedling stage, showed an increased digitalin content of 21 to 40 per cent, although there was no perceptible increase in the amount of growth of the plants. Eltinge ('28) rayed plants with a mercury arc, screened and unscreened, and found in some cases that growth was apparently stimulated when screens were used; she used a screen of vita-glass and one of quartz-lite glass; the former transmits to 289 mμ, the latter to 313 mμ; plants rayed with the vita-glass showed for the most part better growth than those rayed with the quartz-lite; both showed more growth than the controls; when the unscreened lamp was used, only injury occurred. Shortly after this work, Popp and Brown ('28) reported on experiments with some of the plants with which Miss Eltinge had worked; they found only injury under an unscreened lamp; moreover, they found that when the lamp was screened to give wave lengths down to only 300 mμ, no stimulation occurred, nor was there any injury. Fulton and Coblentz ('29) found indications of stimulation on moulds which they exposed to the mercury arc for short periods; when the periods of exposure were increased, injury resulted.

Newell and Arthur ('29) rayed tomato plants with a mercury arc, both unscreened and screened with filters transmitting small progressive portions of the ultra-violet spectrum, and found only injury in the rays shorter than the solar limit; the upper limit at which harmful effects were produced was found to be at 281.1

mμ; in the longer wave lengths (above 290 mμ) there was neither injury nor stimulation. Sheard, Higgins, and Foster ('30) reported the results of experiments on the germination and early growth of seedlings under various portions of the solar spectrum; their results indicated that the ultra-violet and infra-red portions of sunlight are stimulatory to germination and enhance growth and later development, but that they induce less chlorophyll formation than do other portions of the spectrum.

Statement of the Problem and Criticisms of Previous Work

The object of this work is to determine whether or not radiation from a quartz mercury vapor air-cooled arc might cause definite accelerative stimulation in the growth of higher plants, in an endeavor to contribute something positive to the much-controverted subject. Certain criticisms of previous work may be offered which may be of aid in accounting for the discrepancies mentioned in the reviews. In the first place, most workers heretofore have neglected to furnish quantitative measurements of the radiant energy given off by the lamps with which they have worked; obviously differences in respect to this factor can be expected to account for a large portion of the disputed results. Secondly, accurate measurements of the wave lengths given off by the sources of radiation have been omitted in some cases; there can of course be no basis for the comparison of results obtained with a screened lamp transmitting to 300 mμ, with those obtained from an unscreened lamp which transmits, say, to 220 mμ, and yet very often attempts are made to correlate the findings of experiments conducted under such widely divergent conditions, with the result that endless and unnecessary disputes have arisen. In the third place, the methods of exposing the plants to the source of radiation have differed; some workers have rayed plants at a distance of 20 inches from the arc, still others at 100 inches, and so on; further, the periods of irradiation have varied widely, as well as the methods of applying them—some investigators have given the same dosage every day, others have increased the periods gradually throughout a series of daily irradiations, etc. In the last place, the experimental populations have in most cases been too small to make possible the exclusion of individual varia-

tion in interpreting the results; conclusions drawn from the reactions of six or eight plants cannot be of much value. This factor can be overcome only by the use of large numbers of individuals in the experiments; then, too, accurate statistical analyses have not been made of results, with the consequence that the reliability of measurements obtained has not been determined.

In the past, most workers have assumed the effects produced by the mercury and carbon and iron arcs to be due to the ultra-violet spectrum alone. It has been shown by Sheard and Higgins ('27) that the mercury vapor arc may give off as much as one third of its total radiation as infra-red. Hence, it is a flagrant disregarding of facts to assume that the effects of the mercury arc on organisms are due to the ultra-violet region alone. In this paper, the term "ultra-violet" is used to express this limitation—that is, to mean in reality, "the radiation from the mercury arc." In a continuation of the present work, the author intends to study the effects of the radiation from a lamp screened by a quartz water cell to remove the greater portion of the infra-red rays, upon the same plants used in this work.

In the prosecution of this work, an attempt has been made to reduce to a minimum the four objections raised in the second preceding paragraph.

Methods and Materials

The experimental methods used in this work were planned specifically in relation to three recent works on the subject of stimulation of plants by ultra-violet, that of Miss Eltinge ('28), of Popp and Brown ('28), and of Newell and Arthur ('29). Miss Eltinge reported that the radiation from a mercury arc, screened by vita-glass and quartz-lite, "was beneficial" to some of the plants with which she worked—*Cucumis sativus*, var. "Improved Green Hybrid," *Coleus Blumei*, *Bryophyllum pinnatum*, *Lactuca sativa*, and others. Popp and Brown, working on some of the same plants, reported only injurious effects with the unscreened lamp, and neither injury nor stimulation with the lamp screened to remove wave lengths below 300 mμ. Newell and Arthur likewise obtained only deleterious effects with the unscreened lamp in their work on tomatoes; above 281.1 mμ they found neither

injury nor stimulation. It was thought that certain differences in the experimental procedures of Miss Eltinge and of these other investigators might account, in part at least, for the apparently conflicting results, and so the methods they employed were carefully compared in order to devise a technique which might incorporate certain aspects of the methods of all three investigators and which thus might offer some common basis for comparison.

The following differences were noted:

1. Miss Eltinge rayed the plants she used for periods which began with 30 seconds on the first day and which increased by that same amount on each successive day. Popp and Brown, and Newell and Arthur used a constant period for each daily irradiation; no incremental method was used. The periods used by them varied from a few seconds to several hours.

2. Miss Eltinge used the vita and quartz-lite glass screens in her work; Newell and Arthur, and Popp and Brown used filters whose transmissions differed from those used by Miss Eltinge and in addition used the unscreened arc in attempting to find whether or not stimulation occurred.

3. Miss Eltinge rayed her plants at distances of 50 and 100 inches. Popp and Brown used a distance of 50 centimeters, Newell and Arthur a distance of 15 inches.

The experimental work described in this paper was planned upon the basis of these differences in the following manner:

Since the methods of irradiation employed by Miss Eltinge differed from those of Popp and Brown and Newell and Arthur, it was thought that, by using Miss Eltinge's procedures, which she reported to cause stimulation, on the plants employed by these other workers and reported by them to be unstimulated, it might perhaps be possible to accelerate their growth. Accordingly, the plants selected were *Cucumis sativus* L., var. "Early White Spine," used by Popp and Brown, and *Lycopersicum esculentum* Mill., the common tomato, which Newell and Arthur employed in their work. In addition to Miss Eltinge's method of applying the irradiation periods—that of daily increments of 30 seconds—, experiments using equal daily exposure periods were performed to determine whether or not the incremental method might enable the plants to become adjusted to the radiation and

thus to escape injury and perhaps even to derive some benefit from the gradually increased dosages. In order to make certain that any differences resulting from the two methods of dosage would be due only to the difference in the method and not to unequal quantities of energy received, the periods of exposure were planned so that at the end of the experiment the plants rayed according to the two procedures would have received exactly the same amount of radiant energy.

The source of ultra-violet radiation in these experiments was an air-cooled Uviarc quartz-mercury vapor arc from the Burdick Cabinet Co.; throughout the experiments the arc was used at 70 volts with a current of 6 amperes. In some of the work the lamp was unscreened, and in other portions the quartz-lite and vita-glass filters were used. Spectrographs showed that the unscreened lamp gave off radiation ranging from 578 mμ to 200 mμ; when the arc was screened with vita-glass, the ultra-violet spectrum below 289 mμ was removed; when the arc was covered with the quartz-lite filter, the rays below 313 mμ were removed.

In this work two experiments were performed, the first, a preliminary one, intended to "feel out" any tendencies which might become evident, the second, a more exhaustive investigation of the results obtained from the first. In the following discussion, these experiments will be designated as I and II respectively.

In experiment I, the plants were rayed at 50 inches for 4 weeks. The following experimental groups were used:

Set A—Controls.

Set B—Plants rayed, using a quartz-lite filter, for a period of 30 seconds on the first day, increased thereafter by an equal period daily.

Set C—Plants rayed, using a quartz-lite filter, for a period of 7.5 minutes daily.

Set D—Plants rayed with the unscreened arc, with radiation periods as in Set B.

Set E—Plants rayed with unscreened arc, the radiation periods as in Set C.

The groups in experiment I consisted of 15 plants each, a number probably too small to overcome the factor of natural variation in the final interpretation of results but nevertheless

large enough to indicate general trends. The plants were rayed daily, with the periods adjusted to insure equal amounts of energy for the rayed groups. In this experiment the plants were grown individually in 2-inch pots, in a mixture of three-fourths loam and one-fourth sand. The plants were moved about in the greenhouse at the end of each week to insure similar environmental conditions.

In experiment II the plants were rayed at 100 inches for 5 weeks. The experiment consisted of the following groups:

Set A—Controls.

Set B—Plants rayed, using a quartz-lite filter, for a period of 30 seconds on the first day, increased thereafter by 30 seconds daily.

Set C—Plants rayed, using a quartz-lite filter, for a period of 9 minutes daily.

Set D—Plants rayed, using a vita-glass filter, with irradiation periods as in Set B.

Set E—Plants rayed, using a vita-glass filter, with irradiation periods as in Set C.

Each group in experiment II consisted of 100 plants, a number large enough to reduce to a minimum the factor of individual variation.

The heights and numbers of leaves in the plants in both experiments were recorded at the beginning of the experiments, at the end of half the period, and again at the conclusion. In addition, in experiment II, wet weights, dry weights, and ash weights were determined, and from these results the dry weight percentages of wet weight and the ash-weight percentages of dry weight were calculated. In the determination of dry weights, the plants were dried in an oven at 60° C. After the weighings had been completed, the plants were incinerated in porcelain crucibles in a Bunsen flame until the ash fused; the covered crucibles were then placed in a desiccator to cool, in order to exclude the possibility of error from the condensation of atmospheric water vapor upon the ash or crucible. Since the time was not available for making 1,000 individual ash determinations of the plants in experiment II, 30 plants were selected from the control set and 30 from the group which showed the greatest growth under the arc, 10 plants

from among those which showed growth greater than that of the group average, 10 from those which showed growth equal to that of the group average, and 10 from those which showed less growth than the group average.

Intensity measurements were made by means of a Leeds and Northrup high sensitivity type P reflecting galvanometer #2239, with a sensitivity of .7 microamperes, and two Cenco linear thermopiles. A carbon filament incandescent lamp, from the Bureau of Standards of the U. S. Department of Commerce, standardized to give a radiation of 86.2×10^{-8} watts per square millimeter of receiving surface at two meters when lighted at .4 amperes and 99.5 volts, was used as a basis for computing the radiant energy given off by the arc. The intensity measurements are as follows:

At 100 inches:

Unscreened arc—956.44×10^{-8} watts per sq. mm.
Vita-glass —732.70×10^{-8} watts per sq. mm.
Quartz-lite —724.08×10^{-8} watts per sq. mm.

At 50 inches:

Unscreened arc—3825.76×10^{-8} watts per sq. mm.
Vita-glass —2930.80×10^{-8} watts per sq. mm.
Quartz-lite —2896.32×10^{-8} watts per sq. mm.

Observations and Results

EXPERIMENT I

Cucumbers.—The first visible effects on rayed plants appeared in set E, rayed 7.5 minutes daily with the unscreened arc, at the end of a week's period of irradiation. The upper epidermis appeared shiny and there was a slight curling of the younger leaves. Upon examination with a hand lens, it was found that the hairs on the upper epidermis had been completely burned off. These effects rapidly became intensified; after about 12 days the enlargement of young leaves had ceased entirely and all of the leaves of the plant were badly curled. The leaves were stiff and brittle, and showed a slight brownish discoloration of the upper surfaces. At the end of 22 days the plants had practically ceased growing, and death followed a few days later.

In set D, rayed for incremental periods with the unscreened arc, the first manifestations of injury were not as pronounced as

those in set E. The first effects of burning became noticeable on about the twelfth day and became gradually more intense, culminating in death on about the twenty-eighth day. At the time of death, the leaves were somewhat larger and more numerous than those in set E and the plants were somewhat taller. The growth differences are shown in table I at the end of this section.

There were no striking differences between sets A, controls, and B, rayed with the quartz-lite filter for incremental periods, at any time during the experiment, except that some plants in set B were slightly taller than those in set A. Since 9 of the 15 plants in set B were taller than the tallest plants in set A, it seemed that some small amount of stimulation of growth had occurred in set B, but, as has been stated before, the number of plants was not large enough to overcome individual variation. Hence, no definite interpretation can be placed upon the results. The number of leaves in set B was slightly greater than that in set A.

Set C, rayed 7.5 minutes daily with the quartz-lite filter, showed a perceptibly slower rate of growth and a smaller number of leaves than set B. Aside from this, there were no differences between the two sets. Neither showed any injury whatsoever, and the leaf sizes were approximately equal.

It will be seen from the figures in table I that the growth rate in set A during the first two weeks was slightly less than that occurring during the last two weeks of the experiment. In set B the same relationship held, but in set C the growth rate through the last two weeks was less than that of the first two weeks; this condition prevailed in sets D and E also. It is interesting to note that these growth relations were practically identical in the tomato plants.

Tomatoes.—The various experimental groups of tomatoes stood in approximately the same relation to each other as did the cucumber groups. Sets D and E showed the same type of injury as did the cucumbers—burning off of epidermal hairs, discoloration of epidermal tissue, the final cessation of growth, and the death of the plant. The tomatoes seemed slightly more sensitive in their reaction to the unscreened arc than did the cucumbers, for they exhibited signs of injury after about 6 days of irradiation. They ceased growing at about the same time as did the cucumbers,

but they remained alive a few days longer. The injurious effects were less pronounced in set D than in set E, as was also the case in the cucumbers.

The plants in set B showed a slightly increased amount of growth over the controls, and those in set C showed less growth than did set B. Aside from this, there were no differences in the plants in these groups. The growth rates in sets A and B were greater during the last two weeks of the period than during the first two; in sets C, D, and E, the reverse occurred. The similarity of these reactions in both cucumbers and tomatoes seemed to indicate a tendency—that of the repression of growth by ultra-violet radiation when the dosage exceeds an optimum value. This will be discussed later in the paper.

Plate 3, fig. 1, shows the appearance of plants from the five sets of tomatoes at the end of the four weeks of exposure.

TABLE I

CUCUMBERS

Set	Average increase in height of plant and in number of leaves during experiment					
	1st 2 weeks		2nd 2 weeks		4 weeks—total	
	Height	Leaves	Height	Leaves	Height	Leaves
	cm.		cm.		cm.	
A	4.71	2.85	4.92	1.00	9.63	3.85
B	4.64	2.57	5.30	2.21	9.94	4.87
C	4.23	2.57	3.44	1.33	7.67	3.80
D	4.02	2.06	.94	.71	4.96	2.77
E	3.05	2.01	.17	0.00	3.22	2.01

TABLE II

TOMATOES

Set	Average increase in height of plant and in number of leaves during experiment					
	1st 2 weeks		2nd 2 weeks		4 weeks—total	
	Height	Leaves	Height	Leaves	Height	Leaves
	cm.		cm.		cm.	
A	3.99	1.20	6.33	2.00	10.32	3.20
B	4.76	1.87	6.27	1.22	11.03	3.09
C	3.86	2.00	3.20	1.30	7.06	3.30
D	3.02	1.28	1.82	.54	4.84	1.82
E	2.44	1.25	1.25	.40	3.69	1.65

EXPERIMENT II

When indications of stimulation were found in the plants of experiment I, rayed through the quartz-lite filter, it was decided to perform another experiment to study further these stimulatory effects and in addition to study with the aid of the vita-glass filter the effects of the rays between 313 mμ (the quartz-lite limit) and 289 mμ. To overcome errors due to natural variation, the number of plants in each group was increased to 100; the plants were grown in large-sized greenhouse flats, 25 in a flat, in the same soil as was used for experiment I. The following were the experimental groups:

Set A—Controls.

Set B—Quartz-lite filter; rayed 30 seconds the first day and 30 seconds additional on each following day.

Set C—Same as set B, but rayed 9 minutes daily.

Set D—Vita-glass filter; rayed as in set B.

Set E—Vita-glass filter; rayed as in set C.

The experiment was carried through 5 weeks; the plants were rayed at 100 inches. Statistical analyses were made of the results of experiment II to determine their reliability.

Cucumbers.—The growth increases and the various weights are shown in tables IIIa and IIIb. The plants at the beginning of the experiment averaged about 5 cm. in height.

As the figures show, there was not much difference among sets A, B, C, and D, as to growth rate and number of leaves produced. In set E, however, the increase in elongation during the five weeks was significantly greater than that of the controls, about 35 per cent greater. The number of leaves produced in set E was also larger than that of the controls. Aside from these factors, there were no other apparent differences between sets A and E—leaves were of approximately the same size and the numbers of flowers produced in both groups were about equal. There were no evidences of injury in any of the rayed plants. The results of this part of the experiment are shown in plate 3, fig. 2.

Tomatoes.—The tomatoes at the beginning of the experiment averaged about 2.5 cm. in height. The results of the experiment are shown in table ɪᴠa and ɪᴠb, and in plate 3, fig. 3.

Here, as in the cucumbers, there were no great differences among sets A, B, C and D, although in general the rayed sets showed

slightly more growth than the controls, and furthermore the wet and dry weights and the dry percentages of wet weights were slightly greater in the rayed sets. In set E, the growth in height was very definitely greater, by approximately 35 per cent than in the controls. The number of leaves produced in set E was greater than that in set A, and the wet and dry weights and dry-weight percentage of wet were considerably larger. There were no signs of injury in the rayed plants.

In the tomatoes and cucumbers, the rayed sets showed a slightly greater dry-weight percentage and ash-weight percentage. Furthermore, in both plants in experiment II, growth was greater in all of the sets during the last 2½ weeks than during the first 2½. This would seem to indicate that the limit at which there would be repression of growth and injury by ultra-violet radiation had not been reached. The effects of passing that limit are shown by the results of experiment I.

TABLE IIIa

CUCUMBERS

Set	Average increase in height of plant and in number of leaves during experiment					
	1st 2½ weeks		2nd 2½ weeks		5 weeks—total	
	Height	Leaves	Height	Leaves	Height	Leaves
	cm.		cm.		cm.	
A	5.72	2.86	18.54	4.36	24.26	7.22
B	5.25	3.31	22.06	4.41	26.31	7.72
C	5.16	2.87	17.79	3.64	22.95	6.51
D	4.80	2.93	16.26	3.81	21.06	6.74
E	6.18	3.08	26.88	5.61	33.06	8.69

TABLE IIIb

CUCUMBERS

Set	Weights		
	Average wet weight	Average dry % of wet wt.	Average ash % of dry wt.
	gms.		
A	11.75	9.01	18.02
B	11.98	10.01	
C	11.92	9.92	
D	12.02	10.08	
E	14.16	9.98	20.29

TABLE IVa

TOMATOES

Set	Average increase in height of plant and in number of leaves during experiment					
	1st 2½ weeks		2nd 2½ weeks		5 weeks—total	
	Height	Leaves	Height	Leaves	Height	Leaves
	cm.		cm.		cm.	
A	5.91	4.50	13.97	.56	19.88	5.06
B	5.55	4.79	16.12	.80	21.72	5.59
C	5.17	4.62	18.00	1.00	23.17	4.72
D	4.90	3.99	16.81	1.61	21.71	5.60
E	5.67	3.92	21.23	2.19	26.90	6.11

TABLE IVb

TOMATOES

Set	Weights		
	Average wet weight	Average dry % of wet wt.	Average ash % of dry wt.
	gms.		
A	10.52	8.07	16.98
B	11.34	9.65	
C	13.06	9.77	
D	12.44	10.02	
E	15.18	10.45	19.15

Statistical analyses of the increases in length, the dry-weight percentages of wet weights, and the ash-weight percentages of dry weight were made. A $\frac{\text{mean difference}}{\text{probable error diff.}}$ of 4.00 is accepted as indicating complete reliability of results.[1] The values of the analyses are shown below:

[1] Garrett, H. E. Statistics in psychology and education. p. 136. London, 1926.

CUCUMBERS

Set	Height cm.	Dry % of wet wt.	Ash % of dry wt.
$\frac{A}{B}$	18.08	10.14	
$\frac{A}{C}$	32.82	7.03	
$\frac{A}{D}$	13.95	9.29	
$\frac{A}{E}$	54.03	13.65	9.18

TOMATOES

Set	Height cm.	Dry % of wet wt.	Ash % of dry wt.
$\frac{A}{B}$	5.50	5.01	
$\frac{A}{C}$	12.36	5.98	
$\frac{A}{D}$	9.34	9.76	
$\frac{A}{E}$	55.02	18.89	7.15

Discussion

The results of these experiments demonstrate that at least the longer ultra-violet wave lengths—those of the ultra-violet solar spectrum—produce accelerated growth in higher plants when applied in sufficient dosage. The results further show the lethal effects of the shorter wave lengths on the same plants.

Several interesting facts were brought out by the work. The greater stimulation at 100 inches as compared with that at 50 inches is in accord with earlier findings (Eltinge, '28), and may be attributed to the fact that at 50 inches some of the shorter rays, which may pass through the filter and which may be slightly repressive though not destructive to growth processes, reach the plants. At 100 inches, most of these short rays are screened out

or are so diminished in intensity by the atmosphere of the increased distance through which they must pass that they exert none of their inhibitory effects. On the other hand, the differences in effects at the two distances may be merely a function of differences in amounts of radiation received, assuming a stimulatory limit, above which increased radiant energy produces only retardation of growth, or even pronounced injury. The radiation at 50 inches, even if qualitatively about the same as it is at 100 inches, is four times more intense than at 100 inches; hence it is logical to assume that if the radiation at 100 inches is of the proper intensity to induce a high degree of stimulation, the intensity at 50 inches, being, as it were, of four times greater energy value, closely approaches or surpasses slightly the limit of beneficial influences and produces less stimulation than at 100 inches, no stimulation at all, or at the other extreme, retardation.

The use of incremental and constant periods of radiation produced varied and somewhat uninterpretable results. In experiment I, the plants rayed with increments (B—screened, D—unscreened) showed better growth than those rayed for constant daily periods (C—screened, E—unscreened). In set B the growth rate was greater than that of the controls; in set C, the growth rate was less than those of the controls and of set B. At the end of the irradiation period, the plants in set D were taller and the leaves were slightly larger than those in set E; furthermore, the D plants lived a few days longer than did the E plants before succumbing to the lethal action of the ultra-violet radiation.

These differences cannot be accounted for on the basis of different amounts of energy received, since the periods were adjusted to insure equal energy values for all groups in the experiment. Hence the explanation seems to lie in the building up of a resistance in the plants rayed incrementally by means of a gradual increase in dosage, an "accustoming" process, as it were. Since the B plants showed more stimulation, the incremental process (when the lamp is screened) would seem to consist of two reactions: gradual adjustment of the plant to the radiation, followed by accelerated growth. When the lamp is unscreened, the incremental radiation reduces the injury to the plants. The failure of the constant-period method to induce more rapid growth in the

case of the screened lamp may perhaps be due to the fact that without the adjustment process the dosage at the beginning is above the beneficial limit and hence only negative results occur.

The effect of the incremental method, on the other hand, might be explained upon this basis: that during the latter half of the five-weeks radiation period, the plants which were rayed by the incremental method were receiving considerably more energy per day than were those in the constant-period groups; this greater energy coming at a time when the growth rate was rapid may have caused the greater stimulation. This explanation seems to be invalidated, however, by the experiments in which the plants were rayed with the unscreened arc; here during the latter half of the five-weeks period, the plants in the incremental group were likewise receiving more energy per day than those in the constant-period group. If the above explanation were the true one, it would be expected that the plants in the incremental group would show the greater injury, but, as a matter of fact, the plants rayed incrementally showed *less* injury. This would seem to indicate that the resistance theory is more satisfactory.

The necessity of using an incremental method at 50 inches to produce any stimulation whatsoever might explain the negative results of Popp and Brown and of Newell and Arthur in their attempts to discover stimulation in the wave lengths above 300 $m\mu$, since they both worked at distances of less than 50 inches—Popp and Brown at 50 cm., Newell and Arthur at 15 inches.

These explanations, however logically they coincide with the results of experiment I, are not wholly satisfactory when they are applied to experiment II. In the cucumber plants rayed through the quartz-lite filter, the incremental method induced greater growth than did the constant-period method. In all other rayed sets in experiment II, however, both in cucumbers and tomatoes, the reverse was true—the plants rayed incrementally showed less growth than those rayed for constant periods. An explanation of this is wanting. One possible cause—but hardly an important one—may be the fact that the plants used in experiment I were younger than those in experiment II, and that there may be different relations in the adjustment reactions of plants at different

periods in their early development. Another suggestion to explain this variation is difference in wave length. In experiment I, where the increment sets showed the greater growth, the vita-glass filter was not used, but instead, the quartz-lite and the unscreened arc. In experiment II, in the cucumbers, the increment quartz-lite set showed greater growth than the constant-period quartz-lite set; in the tomatoes the reverse was true, but the difference was slight. In both tomatoes and cucumbers rayed through the vita-glass, however, the incremental method showed much less growth than the constant-period method. Hence, it appears as though the quality of the spectrum transmitted by the vita-glass might have caused this variation from conditions in experiment I.

It is interesting to note that not only the growth rates and numbers of leaves produced in rayed plants were greater than in the controls, but that also the dry-weight and ash-weight proportions were greater. The fact that the ash content of the rayed plants showed an increase over the controls is especially interesting, since ultra-violet radiation has been shown also to increase the mineral content, especially the calcium and phosphorus content, of animal tissues in the case of rickets and other deficiency diseases (Kramer and Boone, '22; Orr, Holt, Wilkins and Boone, '23; Ellis and Wells, '25). Beeskow ('27) reported that ultra-violet radiation increases the calcium and phosphorus content of soybeans which are exposed to a mercury arc.

Since greater stimulation occurred under the vita-glass filter than under the quartz-lite, it seems that wave-lengths between 313 mμ and 289 mμ are more potent in inducing growth than those longer than 313 mμ. It might be argued that the difference in stimulation produced by the two filters is a function of varying intensities of the radiation which they transmit; however, the intensity measurements show such slight differences that this argument is seemingly not valid. This agrees with the general findings concerning this shorter portion of the solar spectrum—its greater activity in photochemical processes, its greater efficiency in the treatment of rickets, etc.

Summary

1. The longer ultra-violet wave lengths under certain conditions described in this paper are stimulating to the growth of higher plants.

2. The injurious effects of the short wave lengths have been again demonstrated.

3. Dry weight and ash weight of plants employed in this work increase with ultra-violet treatment.

4. Wave lengths between 313 mμ and 289 mμ produce greater stimulation than those longer than 313 mμ.

5. The incremental method for the most part produces greater growth than the constant-period method, indicating an induced adjustment of the plants to the gradual increase of dosage.

6. The more marked stimulation occurs at a greater distance than that used by most other workers.

7. Statistical analyses proved the reliability of the results.

Acknowledgements

The author expresses his gratitude to Dr. Ernest Shaw Reynolds, of the Henry Shaw School of Botany of Washington University, whose constant interest made possible this work; to Dr. L. A. DuBridge and Mr. L. VanAtta of the physics department of Washington University, who aided with intensity measurements; to Miss Nell Horner, editor of publications of the Missouri Botanical Garden, for her aid with proof-reading; and to Dr. George T. Moore, Director of the Garden, for the use of the library of the Missouri Botanical Garden.

Bibliography

Bailey, L. H. ('94). Electricity and plant growing. Mass. Hort. Soc. Trans. **1894:** 1–28. 1894.

Beeskow, H. C. ('27). Some physiological reactions of ultra-violet rays on plants. Paper at Nashville—Am. Assoc. Adv. Sci. Plant Physiol. Sect. Dec. 1927.

Bonnier, G., et Mangin, L. ('86). L'action chlorophyllienne dans l'obscurité ultra-violette. Acad. Paris, Compt. Rend. **102:** 123. 1886.

Bovie, W. T. ('16). Effect of Schumann region on living organisms. Bot. Gaz. **61:** 1–29. 1916.

Brooks, Matilda M. ('26). Effect of light of different wave lengths on penetration of 2,- 6,-dibromo phenol indophenol into Valonia. Soc. Exp. Biol. and Med. Proc. **23:** 576–577. 1926.

Burge, W. E. ('17). The action of ultra-violet radiation in killing living cells such as bacteria. Am. Jour. Physiol. **43:** 429–432. 1917.

Chauchard, A., et Mazoué, B. ('11). Action des rayons ultra-violets sur l'amylase, l'invertine et la mélange de ces deux diastases. Acad. Paris, Compt. Rend. **152:** 1709–1713. 1911.

Coblentz, W. W., and Fulton, H. R. ('24). A radiometric investigation of the germicidal action of ultra-violet radiation. U. S. Dept. Com., Bur. Stand. Sci. Paper 495: 641–680. 1924.

Coward, K. H. ('27). The influence of light and heat on the formation of Vitamin A in plant tissues. Jour. Biol. Chem. **72:** 781–799. 1927.

Dane, H. R. ('27). The effect of ultra-violet radiation upon soybeans. Science N. S. **66:** 80. 1927.

Delf, E. M., Ritson, K., and Westbrook, A. ('27). The effect on plants of radiations from a quartz mercury vapour lamp. Brit. Jour. Exp. Biol. **5:** 138–141. 1927.

Dufrénoy, J. ('25). Action des radiations ultra-violettes sur les zoospores de Blepharospora cambivora et de Phytophthora omnivora parasitica. Rev. Path. Vég. **12:** 270–272. 1925.

Ellis, C., and Wells, A. A. ('25). The chemical action of ultraviolet rays. New York, 1925.

Eltinge, Ethel T. ('28). The effects of ultra-violet radiation upon higher plants. Ann. Mo. Bot. Gard. **15:** 169–240. 1928.

Euler, J. ('25). Über das Wachstum von Mikroorganismen auf bestrahltem lipoidhaltigen Nahrboden. I. Biochem. Zeitschr. **165:** 23–28. 1925.

Fulton, H. R., and Coblentz, W. W. ('29). The fungicidal action of ultra-violet radiation. Jour. Agr. Res. **38:** 159–168. 1929.

Gibbs, R. D. ('26). The action of ultra-violet light on Spirogyra. Roy. Soc. Canada Trans. **20:** (Sect. 5): 419–426. 1926.

Grantz, I. M. ('98). Einfluss des Lichtes auf die Entwickelung einiger Pilze. Dissertation. Leipzig, 1898.

Green, J. R. ('97). On the action of light on diastase and its biological significance. Roy. Soc. London, Phil. Trans. B**188:** 167–190. 1897.

Hertel, E. ('05). Über physiologische Wirkung von Strahlen verschiedener Wellenlänge. Zeitschr. f. allgem. Physiol. **5:** 95. 1905.

Kluyver, A. J. ('11). Beobachtungen über die Einwirkung von ultra-violetten Strahlen auf höhere Pflanzen. K. Akad. Wiss. Wien, Sitzungsber. **120:** 1137–1170. 1911.

Kramer, J. and Boone, F. H. ('22). The effect of sunlight upon the concentration of calcium and of inorganic phosphorus of the serum of rachitic children. Soc. Exp. Biol. and Med. Proc. **20:** 87–89. 1922.

Laurent, E., et Marchal, E. ('03). Recherches sur la synthese de substance albuminoide par les végétaux. Bruxelles 1903.

Luers, H., und Christoph, H. ('23). Über die Abtötung von Hefe durch ultraviolette Strahlen. Zentralbl. f. Bakt. II. **59:** 8–13. 1923.

McCrea, Adelia ('28). Effect of ultra-violet rays on Digitalis purpurea. Science N. S. **67:** 277–278. 1928.

————, ('29). The effect upon Digitalis purpurea of radiation through solarized ultra-violet transmitting glass. *Ibid.* **69:** 628. 1929.

Maquenne, L., et Demoussy, J. ('09). Influence de rayons ultra-violets sur la végétation des plantes vertes. Acad. Paris, Compt. Rend. **149:** 756. 1909.

Nadson, G., et Philippov, G. ('28). Action excitante des rayons ultra-violets sur le développement des levures et des moisissures. Soc. Biol. Compt. Rend. **98**: 366–368. 1928.

Newell, J. M., and Arthur, J. M. ('29). The killing of plant tissue and the inactivation of tobacco mosaic virus by ultra-violet radiation. Am. Jour. Bot. **16**: 338–353. 1929.

Orr, W. J., Holt, L. E. Jr., Wilkins, L., and Boone, F. H. ('23). The calcium and phosphorus metabolism in rickets, with special reference to ultra-violet ray therapy. Am. Jour. Diseases of Children **26**: 362–372. 1923.

Popp, H. W., and Brown, Florence ('28). Is ultra-violet radiation stimulating to plants? Paper at New York—Am. Assoc. Adv. Sci., Plant Physiol. Sect. 1928.

Russell, E. H., and Russell, W. K. ('27). Ultra-violet radiation and actinotherapy. pp. 170–202. 1927.

Schanz, F. ('18). Wirkungen des Lichtes verschiedener Wellenlangen auf den Pflanzen. Ber. d. deut. bot. Ges. **36**: 619–632. 1918.

————, ('19). Wirkungen des Lichtes verschiedener Wellenlange auf die Pflanzen. Ibid. **37**: 430–442. 1919.

Schulze, J. ('10). Über die Einwirkung der Lichtstrahlen von 280 $\mu\mu$ Wellenlänge auf Pflanzenzellen. Beih. Bot. Zentralbl. **25**: 30–80. 1910.

Sheard, C., and Higgins, G. M. ('27a). The influence of selective and general radiations by a quartz mercury lamp upon germination and growth of seeds. Science N. S. **65**: 282–284. 1927.

————, ————, ('27b). Influence of direct irradiation by a quartz mercury arc lamp upon the germination and growth of certain seeds. Plant Physiol. **2**: 461. 1927.

————, ————, and Foster, W. ('30). The germination of seeds, growth of plants and development of chlorophyll as influenced by selective solar irradiation. Science N. S. **71**: 291. 1930.

Stevens, F. L. ('28). Effects of ultra-violet radiation on various fungi. Bot. Gaz. **86**: 210. 1928.

Stoklasa, A. ('12). Über die Einfluss der ultra-violetten Strahlen auf die Vegetation. Centralbl. f. Bakt. II. **31**: 477. 1912.

Tanner, F. W., and Ryder, E. ('23). Action of ultraviolet light on yeast-like fungi. II. Bot. Gaz. **75**: 309–317. 1923.

Tolomey, ('94). Biedermann's Zentralbl. 106. 1894.

Tsuji, ('18). Stimulation in growth of sugar cane and increase of percentage of sugar on exposure to ultra-violet rays. La. Planter **60**: 413. 1918.

Ursprung, A., und Blum, G. ('17). Über die Schädlichkeit ultravioletten Strahlen. Ber. d. deut. bot. Ges. **35**: 385–402. 1917.

Explanation of Plate

PLATE 3

Fig. 1—Tomatoes—Exp. I

A—Control.
B—Rayed with quartz-lite filter by incremental method.
C—Rayed with quartz-lite filter by constant-period method.
D—Rayed with unscreened arc by incremental method.
E—Rayed with unscreened arc by constant-period method.

Fig. 2—Cucumbers—Exp. II

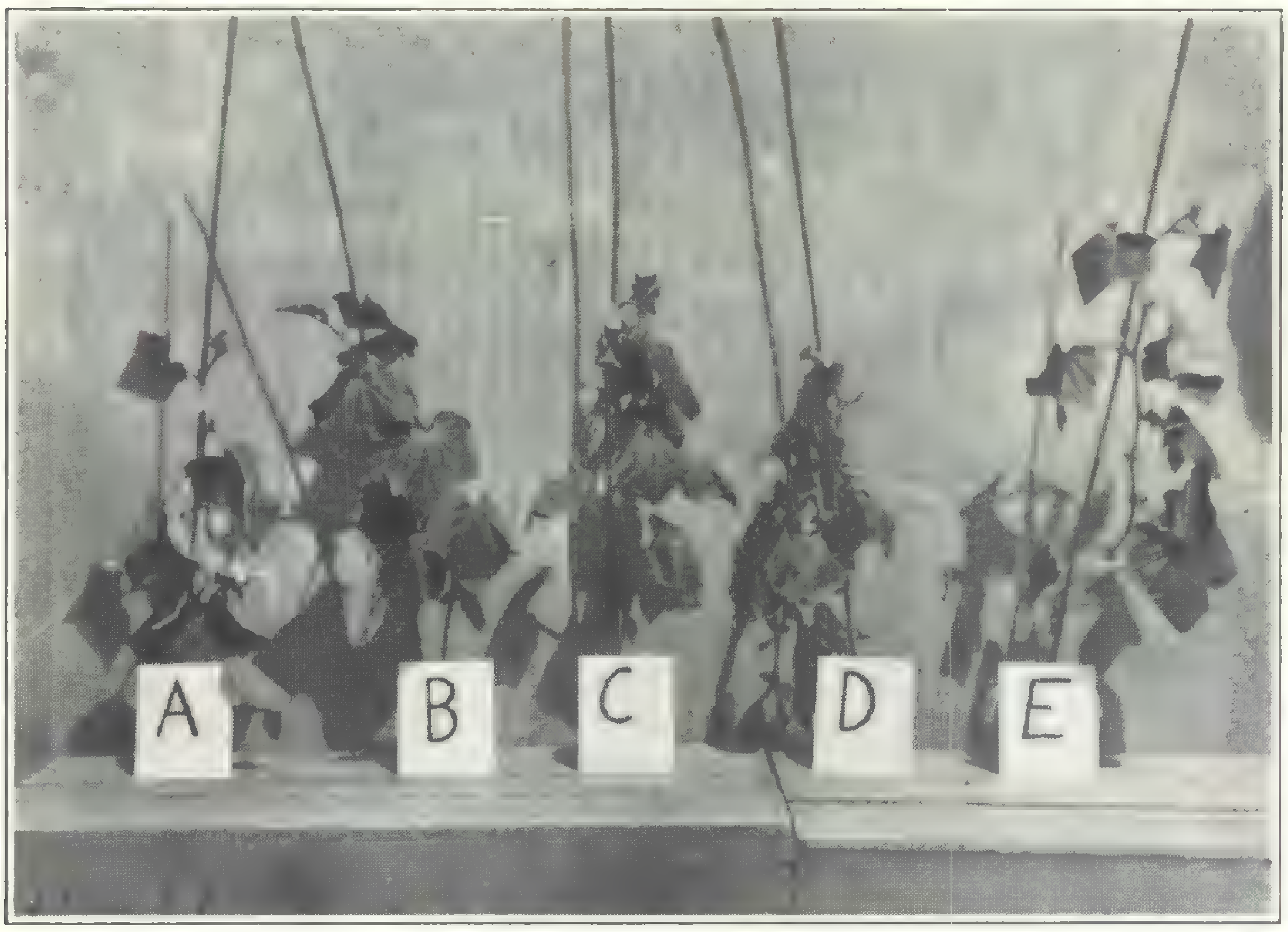
A—Control.
B—Rayed with quartz-lite filter by incremental method.
C—Rayed with quartz-lite filter by constant-period method.
D—Rayed with vita-glass filter by incremental method.
E—Rayed with vita-glass filter by constant-period method.

Fig. 3—Tomatoes—Exp. II

A—Control.
B—Rayed with quartz-lite filter by incremental method.
C—Rayed with quartz-lite filter by constant-period method.
D—Rayed with vita-glass filter by incremental method.
E—Rayed with vita-glass filter by constant-period method.

1

2



3

FULLER—EFFECTS OF ULTRA-VIOLET RADIATION

A STUDY OF PLANT DISTRIBUTION IN RELATION TO THE ACIDITY OF VARIOUS SOILS IN MISSOURI

JULIAN A. STEYERMARK

Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany of Washington University

The various kinds of electrometric and colorimetric methods that have been used to determine hydrogen-ion concentration are all relatively recent. Böttger's work in 1897 on the determination of the neutral point in titrating acids with alkalis by use of a gas chain marked the introduction of electrometric methods, and served as an impetus for subsequent workers, such as Hildebrand, Cumming and Gilchrist, Hasselbalch, Clark, Michaelis, Walpole, and others, each of whom helped to perfect the electrometric method. In 1914 the electrometric method was first applied to the measurement of the hydrogen-ion concentration of soil suspensions by Fischer ('14) in Germany, and subsequently in America by Hoagland and Sharp ('18), and by Gillespie ('16) and his co-workers.

In 1909 Sørensen introduced the colorimetric methods, which were later improved and applied to biological fluids by him, Palitzsch, and Walpole. Further improvements were made by Clark and Lubs ('17) in the use of a different set of indicators and buffer mixtures. Biilmann and Lund, in 1921, showed that with quinhydrone it was possible to form an electrode capable of being used for hydrogen-ion determinations, and in 1923 he ('24) applied this electrode in the determination of the hydrogen-ion concentration of soils. The results compared favorably with those of the hydrogen-electrode method. Before Biilmann's discovery the latter method had proven the most satisfactory electrometric method. However, in recent years the quinhydrone electrode has steadily increased in use, and at present seems for various reasons to be superior to the hydrogen electrode. Bayer's ('26) application of this electrode to soil studies has been followed by a number of other workers. The Report of the Committee on Soil Measurements ('30) of the International Society of Soil Science on the "Results of comparative investigations on the quinhydrone electrode method" shows definitely that this method is at present the most satisfactory one.

In the studies reported here a uniform procedure was followed. Soil samples collected on one day were tested in the laboratory on the day following. In practically all cases a 1:1 soil-water ratio was used, being in most instances 500 grams of soil to 500 cc. of water. The mixture of soil and water was shaken violently for approximately one minute, and subsequently allowed to stand an hour. The supernatant liquid was then poured out, and readings made, four or five of which were taken in almost every determination, so that reliable results might be obtained. After each reading the test-tube vessel and electrode were well rinsed with tap and distilled water. Altogether, twenty-four different soil samples were tested. Only surface soils, taken from a depth of about six inches, were used. For most determinations the samples were collected from areas with typical or conspicuous associations rather than from isolated places exhibiting unusual plants. Seven sets of samples were taken. These comprised two sets from Tilsit soil localities, two from two Hagerstown soil localities, one from a Union soil area, one from the so-called "Rough stony land" area, and a final set from a locality possessing Clarksville stony loam soils. The various names given to these soils are those adopted by the Soil Survey of Missouri.

TILSIT SOILS

The belt of Tilsit, like all the belts along the eastern border of the Ozark dome, is very narrow. The Tilsit soils in Jefferson County are derived from the Crystal City or St. Peter sandstone, which is gray to white, and composed of extremely well-rounded, transparent, coarse quartz grains held together very loosely by a small amount of calcareous cement. This sandstone is subject to severe erosion, and deep gorge-like areas and cliff faces are not uncommon.

Set A.—Three samples were obtained on April 14, 1929, along the high sandstone bluffs back from the Meramec River about five miles southeast of Pacific, Jefferson County, Missouri.

Sample 1. This was obtained on the sandstone bluffs, about five feet from the base. A number of plants of *Lycopodium lucidulum* Michx. were growing on a substratum of *Polytrichum commune* L., mats of which grew on the bare sandstone rock. The pH value of the sample was 4.898.

Sample 2. This was taken at the base of the bluffs where the soil was very sandy, on level ground, in shade. A large colony of *Mertensia virginica* (L.) Link grew here. The soil was slightly subalkaline, having a pH of 8.278.

Sample 3. This soil was taken about thirty feet from the base of the bluffs, and was dark brown and not as sandy as that of the previous sample. It came from near the top of a small slope bordering a stream outlet, where *Dicentra Cucullaria* (L.) Bernh. and *D. canadensis* (Goldie) Walp. grew profusely in dense shade. The soil was circumneutral, being pH 6.588. This is one of the few localities in Missouri for *Dicentra canadensis* (Goldie) Walp.

Set B.—Five samples were obtained on May 12, 1929, about six miles southeast of Catawissa, Missouri. In this region occurred the same formation of sandstone as in Set A, which was approximately six miles north.

Sample 1. This was collected on one of the sandstone bluffs that bordered a ravine. The sample was taken about ten feet from the base of the bluff above a spring, where the sandstone was very loose and crumbly. Growing in abundance were *Sullivantia renifolia* Rosendahl (a species never before reported from Missouri), *Hydrangea arborescens* L., and *Marchantia polymorpha* L. The sample was circumneutral, the pH being 7.65.

Sample 2. This was taken on top of a badly weathered sandstone glade, where the rock was exposed and steeply sloping on the brink of the ravine. The sandy soil was thin and scattered, and never reached a depth of over a few inches. The exposure was dry and sunny. *Talinum teretifolium* Pursh and *Polytrichum commune* L. were the chief plants found. On the day the soil was collected a stream, caused by recent rains, was rushing swiftly down the outcrop near the plants, and was washing away much of the soil. The pH of the soil was 5.85.

Sample 3. This was collected in the floor of a deep ravine bordered by high sandstone bluffs. A shallow stream flowed through the valley. There was a rich deciduous tree growth, which shaded the ground plants. The soil was dark brown to slightly black, quite rich, and contained a fair percentage of sand. On the area from which the sample was taken grew *Orchis spectabilis* L., *Corallorrhiza maculata* Raf., and in the immediate envi-

rons was found *Aplectrum hyemale* (Muhl.) Torr. The soil was neutral, its pH being 7.2. The occurrence here of *Orchis spectabilis* L. is to be noted especially, as it is one of the rarest of Missouri plants.

Sample 4. This was procured from the same valley as Sample 3, but nearer the sandstone bluff and nearer the stream, where the soil was sandier. *Orchis spectabilis* L., *Panax quinquefolium* L., and *Smilacina racemosa* (L.) Desf. grew here. The soil was slightly subalkaline, the pH being 8.26.

Sample 5. This sample was taken above a sandstone ravine, in a situation similar to that of sample 2, but at a lower level and at a spot where more soil had accumulated. The exposure was a sunny, mossy slope above a ravine. Here grew an abundance of *Krigia Dandelion* (L.) Nutt. and *Tradescantia bracteata* Small. The soil was very sandy, and of a yellowish brown hue. The pH of the sample was 5.89.

HAGERSTOWN SOILS

The belt of the Hagerstown series, which occurs along the eastern border of the Ozark dome, like that of Tilsit soils, is very narrow. The soil is derived from the Trenton limestone of middle Ordivician age. The rocks are usually chert-free, finely crystalline, rather hard and compact, and of a dark gray color. In Jefferson County the topography in the Hagerstown belt is rough, and considerable areas of limestone glades occur more or less overgrown with *Juniperus virginiana* L.

Set A.—Five samples were collected on May 5, 1929.

Sample 1. This was collected between Imperial and Seckmann, Missouri, on limestone bluffs which were exposed to the sun and subject to drought. The sample was from cracks or narrow ledges on the rock where a small amount of soil had accumulated. A great abundance of *Cheilanthes Feei* Moore was observed. Plants associated with it were *Aquilegia canadensis* L., *Hydrangea arborescens* L., and *Heuchera hirsuticaulis* (Wheelock) Rydb. The soil was slightly subalkaline, having a pH of 8.482.

Sample 2. This was taken between Imperial and Seckmann, Missouri, in wet soil, in an open valley exposed to the sun and about 30 feet from a road. The soil of the valley floor probably received some alluvial deposits from Rock Creek, a stream about

150 yards distant. It may have also received material from the high limestone hills about 15 yards away, in the opposite direction from that of the stream. The plants found growing in this soil were *Acorus Calamus* L., *Typha latifolia* L., and *Mentha spicata* L. The pH of the soil was 7.285.

Sample 3. This was taken about two miles southwest of Glen Park, Missouri, at the head of a valley leading into a ravine. A stream flowed near by. The woods were dominated by oaks, chiefly *Quercus alba* L. and *Quercus rubra* L. The ground plants growing here were *Erigeron pulchellus* Michx., *Krigia amplexicaulis* Nutt., *Tradescantia bracteata* Small, *Phlox divaricata* L. with a rose-red corolla, and *Cornus florida* L. The soil was free from stones, and had a pH of 6.826.

Sample 4. This was collected about 100 yards from the previous sample, in a dry, mossy, sunny thicket, bordering on open oak woods, near the lower portion of the hill. *Castilleja coccinea* (L.) Spreng. in abundance, *Pedicularis canadensis* L., *Heuchera hirsuticaulis* (Wheelock) Rydb., *Geranium maculatum* L., *Erigeron pulchellus* Michx., *Krigia amplexicaulis* Nutt., *Ranunculus fascicularis* Muhl., and *Polystichum acrostichoides* (Michx.) Schott occurred here. The soil was a light brown clay, stone-free, and was subacid, having a pH of 5.806.

Sample 5. This was collected about one mile northwest of Barnhart, Missouri, near the top of a high, cherty limestone hillside, with a southern exposure, and consequently dry and exposed to the sun. The locality was a glade type, and bordered on a thicket of post oak and black-jack oak. The plants growing here were *Monarda Bradburiana* Beck, *Zizia aurea* (L.) Koch, *Brauneria angustifolia* (DC.) Heller, and *Parthenium integrifolium* L. The pH of the soil was 7.438.

Set B.—There were five samples of soil included in this second set, collected on May 20, 1929. The area was six miles west-southwest of Pevely, and approximately six miles distant from that from which the previous soil samples were taken. This country has considerable areas of limestone glades grown over with *Juniperus virginiana* L.

Sample 1. This was obtained halfway up a limestone hill. The surface limestone was broken into fragments, leaving exposed a

bare rocky glade, with sunny exposure, bordered by cedar trees. *Oxalis violacea* L., *Brauneria angustifolia* (DC.) Heller, *Houstonia longifolia* Gaertn., *Viola pedata* L., *Agave virginica* L., and *Psoralea tenuiflora* Pursh were found here. The soil was subalkaline, its pH being 8.448.

Sample 2. This was collected in rich limestone woods, about halfway up a steep, wooded and densely shaded hill. *Tilia americana* L., *Acer saccharum* Marsh., *Cornus florida* L., *Carya cordiformis* (Wang.) K. Koch, *Ulmus americana* L., and several species of *Quercus* were growing here. Towards the base, massive limestone outcrops occurred. A sample of soil was taken near a huge limestone boulder, where there grew several plants of *Aquilegia canadensis* L. and *Cystopteris bulbifera* L. The soil was dark brown in color and slightly alkaline, its pH being 8.363.

Sample 3. This was taken on the floor of a limestone ravine, near a stream. There was a heavy growth of *Acer saccharum* Marsh., *Ulmus americana* L., *Benzoin aestivale* (L.) Nees, *Aesculus glabra* Willd., and *Quercus alba* L., which shaded the ground plants. *Corallorrhiza maculata* Raf., *Viola striata* Ait., and *Botrychium virginianum* (L.) Sw. were in the immediate vicinity. The soil was a rich stony loam with much humus, and of a dark brown color. It was found to be slightly subalkaline, having a pH of 8.227.

Sample 4. This sample was dug about one-third the way up a thinly shaded hill covered chiefly with several species of *Quercus*, some *Cornus florida* L., and a few species of *Carya*. The soil was dark brown, thickly covered in most places with oak leaves, and was, on the whole, stone-free. The plants found growing here were *Rosa humilis* Marsh., *Antennaria plantaginifolia* (L.) Richards., *Rubus occidentalis* L., *Vaccinium vacillans* Kalm, and *Cunila origanoides* (L.) Britton. The soil was neutral, having a pH of 7.081.

Sample 5. This was collected in soil full of fragments of chert and pure limestone, at the base of a hill covered with oak and hickory. The spot was located just above the bank of a stream and opposite the hill from which the previous sample was collected. The woods here were rather open. The plants found were *Baptisia bracteata* (Muhl.) Ell., *Viola pedata* L., *Monarda Bradburiana*

Beck, *Antennaria plantaginifolia* (L.) Richards., and *Polygonatum commutatum* (R. & S.) Dietr. The soil was of a reddish-brown color, stony, and argillaceous. It was found to be subacid, and its pH 5.89.

UNION SOILS

This comprised a set of soils gathered at Gray Summit, Franklin County, Missouri. The rocks from which the Union soils are derived are the Jefferson City or Beekmantown limestones, of lower Ordivician time; these rocks are a series of moderately cherty, argillaceous, and more or less shaly and thinly bedded limestones. The topography in Franklin County where the Union soils occur is rather rough. All of the samples were collected on slopes where the soil was very shallow and the bedrock was exposed, making limestone glades. *Juniperus virginiana* L. and *Crataegus berberifolia* T. & G. var. *Engelmanni* (Sarg.) Eggleston were collected April 28, 1929. Four soil samples were obtained.

Sample 1. This was obtained under cedar trees, about three-fourths up a slope of a dry, cherty and argillaceous limestone glade. *Dodecatheon Meadia* L., *Astragalus distortus* T. & G., *A. mexicanus* A. DC., and *Lithospermum canescens* (Michx.) Lehm. grew here. The soil was of a yellowish brown color, with a pH of. 8.00.

Sample 2. This sample was dug from dry soil on a slope in cedar woods, about halfway down a hill, where cherty to pure limestone rocks outcropped. The soil was deeper and less rocky here, and of a dark brown color. *Smilax ecirrhata* (Engelm.) Wats., *Polygonatum commutatum* (R. & S.) Dietr., *Botrychium virginianum* (L.) Sw., *Camassia esculenta* (Ker.) Robinson, and *Galium circaezans* Michx. were growing here. The sample was found to be subalkaline, its pH being 8.41.

Sample 3. This was collected on top of a cherty to pure limestone glade, in strong sun, in a large open area surrounded by cedars. The soil consisted almost solely of rock fragments. *Arenaria patula* Michx., *Scutellaria parvula* Michx., *Psoralea tenuiflora* Pursh, and *Petalostemum purpureum* (Vent.) Rydb. were the plant associates. The soil tested was circumneutral, its pH being 8.19.

Sample 4. This was from a similar locality to that of the previous sample, except that the glade was wider and cedars were

found only below and above the barren rock portion. Here were found *Oenothera missouriensis* Sims, *Viola pedata* L., *Sisyrinchium angustifolium* Mill., *Hypoxis hirsuta* (L.) Coville, *Brauneria angustifolia* (DC.) Heller, and *Coreopsis lanceolata* L. The soil was dry, exposed to the sun, and pure limestone rock predominated. It was found to have the same pH as that of sample 1, namely, pH 8.00.

ROUGH STONY LAND SOIL

The soil group classed under this head is derived from igneous rocks consisting of granites, rhyolites, trachytes, and diabase, the most abundant being a dense, hard porphyritic trachyte. The topography of this region is very rough.

One sample was collected from an area opposite Pilot Knob, in Iron County, on April 21, 1929.

Sample 1. This was from a dry sunny hillside opposite Pilot Knob, about a quarter of the distance up a 400-foot slope. It was taken from between rocks of porphyritic trachyte, surrounded by huge boulders. The trees consisted chiefly of second- and third-growth oak and hickory. The ground plants found here associated were *Tradescantia brevicaulis* Raf., *Vaccinium arboreum* Marsh., *Viola pedata* L., and *V. palmata* L. The soil was grayish brown in color, and its pH was 7.089.

CLARKSVILLE SOILS

These soils are mainly stony loams and are derived from the upper Cambrian (Ozarkian) beds of Gasconade cherty limestone, with a basal formation of Gunter sandstone. The areas of Clarksville soils are the most thoroughly dissected of any of the important soil areas of the Ozark dome. One sample was obtained through the kindness of Miss Marion Child, who dug it in Pulaski County, about twelve miles southwest of Dixon, on March 31, 1929.

The sample was obtained on top of a sun-exposed bluff which faced the Gasconade River. There were outcroppings of the Gunter sandstone, and the soil was a fine, sandy, cherty loam, brownish-red in color. Red cedars grew plentifully in the area. Other plants found here were *Verbena canadensis* (L.) Britton, *Lithospermum canescens* (Michx.) Lehm., and *Verbascum Thapsus* L. The soil was circumneutral, its pH being 7.819.

It will be seen from the foregoing account of the work that most of the soils ranged from minimacid to subalkaline, only five of the twenty-four soils tested showing any marked acidity.

No broad generalizations can be made from the limited range of the present piece of work, since the soils were obtained from comparatively few areas, and none was worked in detail. The effort in this investigation was to obtain a reconnaissance of the soil acidities of eastern Missouri, with a list of some characteristic plants on each soil type.

As stated by others, the fact that a given plant is found in soils of a certain degree of acidity or alkalinity does not necessarily indicate that the pH concentration is the all-important factor in determining where the plant grows; nor even that it acts directly upon the plant. It is the opinion of plant physiologists generally that the question of pH has been unduly emphasized as the dominant factor in plant distribution in relation to soil acidity. It appears more and more evident that the distribution of any given plant is the result of a number of factors; of these factors soil acidity or alkalinity and its relationship with hydrogen-ion concentration may be of significance or it may not.

Wherry ('20) has shown that plants grow in nature only when the hydrogen-ion concentration is within certain limits. Sometimes the range may be quite large, and at other times quite narrow. Arrhenius ('20) has studied the "Skärs" around Stockholm, Sweden, and he finds that among the factors influencing plant distribution hydrogen-ion concentration plays a very important rôle. Atkins ('22), in Ireland, is another to have studied the relation between plant distribution and soil acidity. Braun-Blanquet ('24), studying the vegetation of the Mediterranean, found that the hydrogen-ion concentration seems to be the factor in determining the distribution of the so-called calcicoles (lime-growers) rather than the lime. It is thus seen that several investigators in widely separated places have found that plants in nature are greatly influenced by the active acidity of the soil.

Wherever possible the results of the present work were compared with those of Wherry, and in most cases the results checked well. In a number of instances, however, it was found that whereas Wherry had placed a species in a definite class, the present

work indicated that this species is more or less indifferent and grows in a wide acid range. For instance, *Viola pedata* L. is almost always referred to as a subacid to minimacid soil plant, whereas the present work showed it has a range from pH 5.89 to pH 8.448, or in other words, from subacid to decidedly subalkaline. Time and again, *Viola pedata* L. was found on limestone substratum, a fact that would indicate alkalinity. In the case of this plant, which grows usually in dry, sunny, rocky or mossy places, the question appears to be one concerned with water content in the soil rather than of soil acidity.

Other examples of apparent differences are as follows: (1) *Botrychium virginianum* (L.) Sw. is classified as a subacid soil plant; the present work shows this species taking subalkaline conditions. (2) *Hypoxis hirsuta* (L.) Coville and *Lithospermum canescens* (Michx.) Lehm., usually classified as subacid soil plants, were found to take minimalkaline conditions.

There are other apparent instances, also. The present work would lead the writer to believe that there are many plants it would be erroneous to treat as of a definite soil type, for results show that usually these plants are indifferent towards soil pH and will accept quite a range of acidity and alkalinity. Such plants, it is felt, seem to be influenced greatly by water content of the soil or by a combination of other factors, in addition to that of soil acidity. In some cases, it seems unquestionably true that the distribution of certain plants is affected by the soil acidity; in some cases this soil acidity can be traced back to the water relationship in the soil, and in others it cannot. On the other hand, very often the factor of soil acidity does not seem to be the most important one to be considered. It would seem that a number of factors in certain combinations or ratios have much to do with affecting the distribution of a plant, rather than any single factor, such as that of soil acidity.

This work was carried on in the spring of 1929 in the Plant Physiological Laboratory of Washington University, under the kind supervision of Dr. E. S. Reynolds.

COMPARISONS BETWEEN WHERRY'S SOIL ACIDITY RESULTS AND THOSE OF THE PRESENT WORK

Plant	Soil type	Acidity found in present work	Acidity found by Wherry
Lycopodium lucidulum Michx.	Tilsit	pH 4.898 (mediacid)	
Castilleja coccinea (L.) Spreng.	Hagerstown	pH 5.806 (subacid)	
**Krigia amplexicaulis* Nutt.	Hagerstown	pH 5.806 (subacid)	
Pedicularis canadensis L.	Hagerstown	pH 5.806 (subacid)	Minimacid
**Heuchera hirsuticaulis* (Wheelock) Rydb.	Hagerstown	pH 5.806 (subacid)	Indifferent
Geranium maculatum L.	Hagerstown	pH 5.806 (subacid)	Indifferent
**Erigeron pulchellus* Michx.	Hagerstown	pH 5.806 (subacid)	Indifferent
Polystichum acrostichoides (Michx.) Schott	Hagerstown	pH 5.806 (subacid)	Indifferent
Ranunculus fascicularis Muhl.	Hagerstown	pH 5.806 (subacid)	Minimacid
Talinum teretifolium Pursh	Tilsit	pH 5.85 (subacid)	
Polytrichum commune L.	Tilsit	pH 5.85 (subacid)	
Krigia Dandelion (L.) Nutt.	Tilsit	pH 5.89 (subacid)	
**Tradescantia bracteata* Small	Tilsit	pH 5.89 (subacid)	
Baptisia bracteosa (Muhl.) Ell.	Hagerstown	pH 5.89 (subacid)	
**Viola pedata* L.	Hagerstown	pH 5.89 (subacid)	Subacid and Minimacid
**Monarda Bradburiana* Beck	Hagerstown	pH 5.89 (subacid)	
**Antennaria plantaginifolia* (L.) Richards.	Hagerstown	pH 5.89 (subacid)	Minimacid
**Polygonatum commutatum* (R. & S.) Richards.	Hagerstown	pH 5.89 (subacid)	
Dicentra canadensis (Goldie) Walp.	Tilsit	pH 6.58 (circum-neutral)	Circumneutral
Dicentra Cucullaria (L.) Bernh.	Tilsit	pH 6.58 (circum-neutral)	Circumneutral
Phlox divaricata L.	Hagerstown	pH 6.826 (circum-neutral)	Circumneutral
**Erigeron pulchellus* Michx.	Hagerstown	pH 6.826 (circum-neutral	Circumneutral
**Krigia amplexicaulis* Nutt.	Hagerstown	pH 6.826 (circum-neutral)	Circumneutral
**Tradescantia bracteata* Small	Hagerstown	pH 6.826 (circum-neutral)	Circumneutral
Cornus florida L.	Hagerstown	pH 6. 826(circum-neutral)	Minimacid
Rosa humilis Marsh.	Hagerstown	pH 7.081 (neutral)	
Vaccinium vacillans Kalm	Hagerstown	pH 7.081 (neutral)	Subacid
**Antennaria plantaginifolia* (L.) Richards.	Hagerstown	pH 7.081 (neutral)	Minimacid
Cunila origanoides (L.) Britton	Hagerstown	pH 7.081 (neutral)	
Rubus occidentalis L.	Hagerstown	pH 7.081 (neutral)	
Tradescantia brevicaulis Raf.	"Rough stony land"	pH 7.089 (neutral)	Subacid
Vaccinium arboreum Marsh.	"Rough stony land"	pH 7.089 (neutral)	
**Viola pedata* L.	"Rough stony land"	pH 7.089 (neutral)	Subacid or Minimacid
Viola palmata L.	"Rough stony land"	pH 7.089 (neutral)	
Orchis spectabilis L.	Tilsit	pH 7.2 (neutral	Circumneutral
Aplectrum hyemale (Muhl.) Torr.	Tilsit	pH 7.2 (neutral)	
**Corallorrhiza maculata* Raf.	Tilsit	pH 7.2 (neutral)	

Plant	Soil type	Acidity found in present work	Acidity found by Wherry
Acorus Calamus L.	Hagerstown	pH 7.285 (neutral)	
Mentha spicata L.	Hagerstown	pH 7.285 (neutral)	
Typha latifolia L.	Hagerstown	pH 7.285 (neutral)	
**Monarda Bradburiana* Beck	Hagerstown	pH 7.438 (circumneutral)	
Zizia aurea (L.) Koch	Hagerstown	pH 7.438 (circumneutral)	Circumneutral
Parthenium integrifolium L.	Hagerstown	pH 7.438 (circumneutral)	
**Brauneria angustifolia* (DC.) Heller	Hagerstown	pH 7.438 (circumneutral)	
Sullivantia renifolia Rosendahl	Tilsit	pH 7.65 (circumneutral)	Indifferent for *S. Sullivantii* (T. & G.) Britton
**Hydrangea arborescens* L.	Tilsit	pH 7.65 (circumneutral)	
Marchantia polymorpha L.	Tilsit	pH 7.65 (circumneutral)	
Hypoxis hirsuta (L.) Coville	Union	pH 8.00 (circumneutral)	Subacid
Sisyrinchium angustifolium Mill.	Union	pH 8.00 (circumneutral)	
Oenothera missouriensis Sims	Union	pH 8.00 (circumneutral)	
**Brauneria angustifolia* (DC.) Heller	Union	pH 8.00 (circumneutral)	
**Viola pedata* L.	Union	pH 8.00 (circumneutral)	Subacid or minimacid
Dodecatheon Meadia L.	Union	pH 8.00 (circumneutral)	Circumneutral
Astragalus distorta T. & G.	Union	pH 8.00 (circumneutral)	
Astragalus mexicanus A. DC.	Union	pH 8.00 (circumneutral)	
**Lithospermum canescens* (Michx.) Lehm.	Union	pH 8.00 (circumneutral)	Minimacid
Arenaria patula Michx.	Union	pH 8.19 (circumneutral)	
Scutellaria parvula Michx.	Union	pH 8.19 (circumneutral)	
**Psoralea tenuiflora* Pursh	Union	pH 8.19 (circumneutral)	
Petalostemum purpureum (Vent.) Rydb.	Union	pH 8.19 (circumneutral)	
Corallorrhiza maculata Raf.	Hagerstown	pH 8.227 (slightly subalkaline)	
Viola striata Ait.	Hagerstown	pH 8.227 (slightly subalkaline)	
**Botrychium virginianum* (L.) Sw.	Hagerstown	pH 8.227 (slightly subalkaline)	Subacid
Orchis spectabilis L.	Tilsit	pH 8.26 (slightly subalkaline)	Circumneutral
Smilacina racemosa (L.) Desf.	Tilsit	pH 8.26 (slightly subalkaline)	Indifferent
Panax quinquefolium L.	Tilsit	pH 8.26 (slightly subalkaline)	

Plant	Soil type	Acidity found in present work	Acidity found by Wherry
Mertensia virginica (L.) Link	Tilsit	pH 8.278 (slightly subalkaline)	Circumneutral
**Aquilegia canadensis* L.	Hagerstown	pH 8.363 (subalkaline)	Circumneutral
Cystopteris bulbifera L.	Hagerstown	pH 8.363 (subalkaline)	Circumneutral
Smilax ecirrhata (Engelm.) Wats.	Union	pH 8.41 (subalkaline)	
**Polygonatum commutatum* (R. & S.) Dietr.	Union	pH 8.41 (subalkaline)	
**Botrychium virginianum* (L.) Sw.	Union	pH 8.41 (subalkaline)	Subacid
Camassia esculenta (Ker.) Robinson	Union	pH 8.41 (subalkaline)	
Galium circaezans Michx.	Union	pH 8.41 (subalkaline)	
**Psoralea pedunculata* Pursh.	Hagerstown	pH 8.448 (subalkaline)	
Agave virginica L.	Hagerstown	pH 8.448	
**Viola pedata* L.	Hagerstown	pH 8.448	Subacid
Houstonia longifolia Gaertn.	Hagerstown	pH 8.448	
Oxalis violacea L.	Hagerstown	pH 8.448	Indifferent
Cheilanthes Feei Moore	Hagerstown	pH 8.482	Circumneutral to subacid
**Aquilegia canadensis* L.	Hagerstown	pH 8.482	Circumneutral
**Hydrangea arborescens* L.	Hagerstown	pH 8.482	
**Heuchera hirsuticaulis* (Wheelock) Rydb.	Hagerstown	pH 8.482	Indifferent

* Denotes wide range of pH.

Bibliography

Arrhenius, O. ('20). Öcologische Studien in den Stockholmer Schären. Stockholm. 1920. [Cited by Atkins, '22.]

Atkins, W. R. G. ('22). Some factors affecting the hydrogen-ion concentration of the soil and its relation to plant distribution. Royal Dublin Soc., Sci. Proc. **16**: 369–413.

Bayer, L. D. ('26). The use of the quinhydrone electrode for measuring the hydrogen-ion concentration of soils. Soil Sci. **21**: 167–179. 1926.

Biilmann, E. ('24). On the measurement of hydrogen-ion concentrations in soil by means of the quinhydrone electrode. Jour. Agr. Sci. **14**: 232–239. 1924.

————, et Lund, H. ('21). Sur l'electrode à quinhydrone. Ann. de Chim. IX. **16**: 321–340. 1921.

Böttger, W. ('97). Die Anwendung des Elektrometres als Indikator beim Titrieren von Säuren und Basen. Zeitschr. f. phys. Chem. **24**: 253–311. 1897.

Braun-Blanquet, J. ('24). Etudes sur la végétation méditerranéenne. III. Concentration en ions H et calcimétrie du sol de quelques associations de la garigue languedocienne. Soc. Bot. France, Bull. **71**: 639–647. 1924.

Brioux, C., et Pien, J. ('25). Emploi de l'electrode à quinhydrone pour la détermination du P_H des sols. Acad. Paris, Compt. Rend. **181**: 141–143. 1925.

Clark, W. M. ('20). The determination of H-ions. Baltimore, 1920.

Clark, W. M., and Lubs, H. A. ('17). The colorimetric determination of hydrogen ion concentration and its applications in bacteriology. Jour. Bact. **2:** 109, 191. 1917.

Committee on Soil Reaction Measurements ('30). Report, Part I. Results of comparative investigations on the quinhydrone electrode method. Internat. Soc. Soil Sci., Suppl. to Proc. **2.** 1930.

Coville, F. V. ('10). Experiments on blueberry culture. U. S. Dept. Agr., Bur. Pl. Ind. Bull. 193: 1–100. 1910.

Fischer, G. ('14). Die Säuren und Kolloide des Humus. Kühn-Arch. **4:** 1–136. 1914.

Gillespie, L. J. ('16). The reaction of soil and measurements of hydrogen-ion concentration. Wash. Acad. Sci., Jour. **6:** 7–16. 1916.

Gustafson, F. G. ('26). Plant distribution as affected by hydrogen-ion concentration of the soil. Mich. Acad. Sci. Papers **6:** 237–246. 1926.

Hilbig, R. ('26). Der Einfluss der Bodenreaktion auf das Wachstum der Pflanzen. Bot. Arch. **15:** 385–423. 1926.

Hoagland, D. R., and Sharp, L. T. ('18). Relation of carbon dioxide to soil reaction as measured by the hydrogen electrode. Jour. Agr. Res. **12:** 139–148. 1918.

La Mer, V. K., and Parsons, T. R. ('23). The application of the quinhydrone electrode to electrometric acid-base titrations in the presence of air and the factors limiting its use in alkaline solutions. Jour. Biol. Chem. **57:** 613–631. 1923.

Leffmann, H. ('24). Hydrogen-ion concentration in relation to animal and plant growth. Franklin Inst., Jour. **197:** 741–756. 1924.

Marbut, C. F. ('11). Soil reconnaissance of the Ozark region of Missouri and Arkansas. U. S. Dept. Agr., Bur. Soils, Field Operations Rept. **13:** 1727–1873. 1911.

Olsen, C. ('23). Studies on the hydrogen-ion concentration of the soil and its significance to the vegetation, especially to the natural distribution of plants. Carlsb. Lab., Compt. Rend. **15:** 1–166. 1923.

Powers, W. L. ('27). The effect of hydrogen-ion concentration on the growth of certain plants. Soil Sci. **24:** 1–7. 1927.

Salter, R. M., and Morgan, M. F. ('23). Factors affecting the soil reaction. I. Soil-water ratio. Jour. Phys. Chem. **27:** 117–140. 1923.

Salisbury, E. J. ('22). Stratification and hydrogen-ion concentration of the soil in relation to leaching and plant succession with special reference to woodlands. Jour. Ecol. **9:** 220–240. 1922.

Schollenberger, C. J. ('25). An improved calomel electrode. Indus. and Engin. Chem. **17:** 649. 1925.

Sørensen, S. P. L. ('09). Études enzymatiques. II. Sur la mesure et l'importance de la concentration des ions hydrogène dans les réactions enzymatiques. Carlsb. Lab., Compt. Rend. **8:** 1–168. 1909.

Trümpener, E. ('26). Über die Bedeutung der Wasserstoffionenkonzentration für die Verbreitung von Flechten. Beih. bot. Centralbl. **42**[1]**:** 321–354. 1926.

Waksman, S. A. ('24). Influence of soil reaction upon the distribution of filamentous fungi in the soil. Ecol. **5:** 54–59. 1924.

Wherry, E. T. ('18). The reaction of the soils supporting the growth of certain native orchids. Wash. Acad. Sci., Jour. **8:** 589–598. 1918.

————, ('20a). Correlation between vegetation and soil acidity in southern New Jersey. Acad. Nat. Sci. Phila., Proc. **72:** 113–119. 1920.

Wherry, E. T. ('20b). Observations on the soil acidity of Ericaceae and associated plants in the middle Atlantic States. *Ibid.* 84–111. 1920.

————, ('20c). Plant distribution around salt marshes in relation to soil acidity. Ecol. **1**: 42–48. 1920.

————, ('20d). The soil reactions of certain rock ferns. I. Amer. Fern Jour. **10**: 15–22. 1920.

————, ('20e). Soil tests of Ericaceae and other reaction-sensitive families in northern Vermont and New Hampshire. Rhodora **22**: 33–49. 1920.

————, ('22). Soil acidity—its nature, measurement and relation to plant distribution. Smiths. Inst., Ann. Rept. **1920**: 247–268. 1922.

————, ('27a). Determining soil acidity and alkalinity by indicators in the field. Wash. Acad. Sci., Jour. **10**: 217–223. 1927.

————, ('27b). The soil-reaction preferences of certain plant orders. *Ibid.* **17**: 148–149. 1927.

————, ('27c). The soil reactions of some saprophytic orchids. *Ibid.* 35–38. 1927.

STUDIES ON THE PHYSIOLOGY OF PLANT DISEASE

ERNEST S. REYNOLDS

Physiologist to the Missouri Botanical Garden

Associate Professor in the Henry Shaw School of Botany of Washington University

I. General Considerations

The study of the physiology of plant disease has been rather incidental to the work of the pathologist although of basic significance both theoretically and practically. Considerable material concerning the subject is scattered throughout botanical writings, and in recent articles references to various portions of it are made indiscriminately. Many contradictions, real or apparent, are accepted because no discriminating summarization is available, and as a result the objectives of investigation are often vague. A very urgent need exists for a thorough survey of the field, together with a careful consideration of the bearings of recent investigations in the contributory lines of work.

Because the subject is extremely complex it is especially necessary to separate clearly from one another the various questions involved. In many diseases parasitism does not exist, and a careful study of the physiology of such abnormal conditions in contrast with the normal physiology of the plant is especially important. In the study of parasitic diseases the parasite, the host, and the host-parasite complex must be studied separately in relation to the environment. This means, among other things, a better knowledge of the nutritional habits of each disease-producing fungus, although it must be recognized that the substances which a fungus may use as food are often much more numerous than those with which it can come in contact in nature. Here again the scattered information should be brought together and carefully analyzed as a basis for further study.

Such suggestions as we have concerning resistance, at the present time, indicate that there are several types which form a more or less closely graded series. We should scarcely look for any generalization to explain so complex a set of phenomena, nor should we deceive ourselves in the use of such a broad term as "resistance," into expecting to discover some such generalization. Perhaps one of the most frequent mistakes among scientists is to

discover some new law or generalization and then attempt to apply it to many different series of facts. Because natural selection is an important fact of nature we should not attempt to ascribe all evolution to its action. Similarly because we recognize that resistance may be due, in certain cases, to toxic materials, we should not discard the evidence of probable morphological causes in other cases, nor should we fail to recognize that several independent causes may operate conjointly.

At least two rather different classes of disease, as regards resistance, should be differentiated on the basis of the type of parasitism. Certain diseases, such as the rusts, smuts, and powdery mildews, as well as others less well known, are caused by fungi which either cannot grow at all in artificial culture media such as we usually prepare, or if so it is only in a limited portion of their life history and they will not complete their life cycle under such conditions. These are the diseases caused by obligate parasites. Other diseases are caused by fungi which may more or less readily be cultivated as saprophytes in culture media throughout a large portion, if not all, of their vegetative life and often their reproductive phases. Such fungi, which usually are saprophytic but may attain a parasitic life, or on the other hand usually are found as parasites but may be cultivated as saprophytes, are referred to as facultative organisms. We should expect to find intermediate conditions between these two general types of disease, but for clarity of vision it is often well to differentiate sharply the extremes of even a continuous, progressive series.

Resistance in diseases due to obligate parasites may be quite different from that in diseases due to the semi-parasitic, semi-saprophytic fungi. The obligate parasites appear to have been associated with their hosts for long periods of time, resulting in their having become highly specialized to them. This suggests in turn a probability that they are rather stable in their needs and their life habits. If the observations of Stakman, Parker and Piemeisel ('18) concerning the black stem rust of wheat are to be taken as typical of the obligate parasites, some evidences are before us that there is little or no mutation of these fungi taking place now. On the other hand, Leonian's studies ('29), together with others, indicate that the opposite is true of the wilt fungi and

other partial parasites. Their specialization also is less marked in general. Resistance to such omnivorous feeders may well be quite different from immunity or resistance to the highly specialized obligate parasites. Since all organisms are somewhat plastic in their environment the similar effect of environment upon the parasitic relationship in these two classes of disease need not be considered as an argument against the main thought just expressed. The possibility or even probability that in at least some diseases of the facultative-parasitic group mutations of the pathogene may occur disturbs our feeling of security in obtaining resistant varieties by breeding. This should stimulate us to study the causes of resistance, thus having at hand further knowledge to aid us in the fight against possibly saltating parasitic qualities.

We recognize that in some types of disease avoidance the causative organism is excluded so that it does not enter the so-called resistant variety. Thus McLean ('21) reports that in the Mandarin orange, which does not take the citrus canker disease, the stomata are so constructed that they prevent entrance of water and of the bacteria. When the epidermis is injured and the bacteria enter, the supposedly immune variety becomes diseased. Such mechanical conditions seem to be illustrated again in the maturing tomato skin (Rosenbaum and Sando, '20). The fruit develops a thicker cuticle which resists more and more, either the puncturing of a needle or that of the germ-tube of *Macrosporium tomato*. Other kinds of disease avoidance are accomplished through early maturing of varieties, or the absence of insect carriers. Hardly either of these latter types should be called true resistance.

A considerable number of fairly well-authenticated cases are now known in which susceptibility to disease is in direct proportion to the general degree of loss of vegetative vigor. Thus Jones ('99, '05) early reported that the late blight fungus attacks potatoes at the so-called "critical" period of the life of the host, when the greatest drain occurs upon the life processes. The resistance of "Little Jess" wheat to rust is reported by Weston ('27) as breaking down when this variety is attacked by the bunt fungus; and other varieties of wheat likewise become more heavily rusted under attack from bunt. Is resistance more common

among the wild than among the cultivated plants, as has been suggested by some, or the reverse as others have believed? Assuming a struggle for existence, we would expect the wild plants to show the greater resistance, since cultivated ones, while perhaps not lower in vitality, as some have supposed, have been selected by primitive man for other reasons than disease resistance and the latter quality has been more or less lost in the process. Natural selection has resulted in disease resistance among wild plants where these have come in contact with the pathogene. Rapidly growing, vigorous plants frequently are more subject to fungous attack than those of the same species which are slow growing. If resistance is at times due to the presence of some specific, toxic substance it is entirely possible that the reason for the ease of attack on rapidly growing specimens is because this characteristic toxin has not accumulated as rapidly as it can accumulate in slower growing individuals. Metabolic processes resulting in characteristic biochemical products do not always proceed at the same pace as the growth processes which result in enlargement. It is not probable, however, that plants in a condition of reduced vitality are often less subject to invasion, although statements with that implication appear from time to time. These are usually based upon observations, often among rust diseases, which indicate that the hosts which are not carrying on rapid photosynthesis are less vigorously attacked by the pathogene. Doubtless the greater abundance of food in those hosts with active photosynthesis would account for the greater growth of the parasite. Practical criteria for recognition of general physiological, potential vitality or vigor, as contrasted with rapid growth and active photosynthesis, might eliminate these cases from the field of resistance studies.

The usual inability of a pathogene to infect many different kinds of plants need not be due to any particular "resistance" on the part of the unattacked plants, but simply to a complete non-relationship between them and the fungus. No doubt a careful survey would show that many of the fungi which are semiparasitic could be induced to grow upon numerous plants not naturally their hosts and cause disease in these new hosts. Thus new relationships would become established. Massee ('25) pro-

duced parasitic life habits in pure saprophytes by first cultivating them on leaves of plants injected with sugar for several generations and then finally upon the same kinds of leaves without the sugar injection. He also cites the case of the fungus *Dendryphium* which is a pure saprophyte, but which under exceptional conditions in the greenhouse was able to assume a parasitic life upon the cucumber and cause disease injury. Kunkel ('26), it would seem, has established a condition somewhat similar to induced parasitism in his transference of Aster yellows to many plants not naturally subject to the disease, and Young ('26) has made a similar study for several facultative parasites.

Parasitism is a struggle between two organisms, which may be over-balanced by the environmental complex in one direction and result in death or serious injury to the host. It may similarly be over-balanced in the other direction either by external environment or by internal conditions and result in various degrees of resistance; or the balance may be essentially even, in which case such organisms are rather well adjusted to one another and little injury results. Lichens may be suggested as examples of the balanced condition. There are all grades between the two extremes. How then, since environment plays such an important rôle, may we speak of some specific quality, character, or substance as "the cause" of resistance? We are all well aware that in animal and plant parasitic diseases certain causative organisms must be present before the disease occurs. We also know that in most cases certain environmental and internal conditions must be present in addition. Nevertheless we call the specific pathogene "the cause" of the disease. In quite a similar manner it may be possible to pick out of the complex of conditioning phenomena of resistance to a given disease, one factor without which no combination of external environmental factors could cause resistance. This would be called similarly "the cause" of resistance. This may be thought of as the inherent, hereditary quality analogous to "height" as a genetic character, which is subject to such wide fluctuations that an individual of one height-class may be somewhat taller or shorter than some individuals of a neighboring height-class. The discovery of this hereditary cause of resistance in any specific case would not end the problem, since the relative

importance of the various external factors should be clearly estimated. This requires a physiological study of the effects of the disease upon the host as well as what we may call the predisposing causes of the disease. Jones ('26) has recently well outlined the necessary coöperative spirit by which rapid production of resistant varieties may take place, and such coöperative spirit would greatly aid in the general study of the physiology of plant disease.

A considerable portion of the observations in the past upon resistant varieties is invalidated by our present knowledge that there are biological variants of the causal organisms; and that different environmental conditions may quite over-balance the hereditary factor. It will be especially necessary as an early step in the analysis of the general problem to determine anew under what definite conditions each variety is resistant. Then the biochemical and physiological circumstances of resistance may more readily be determined. Much of the contradictory evidence concerning the cause of resistance may be cleared away by studying carefully individual pure lines as regards host resistance in relation to the various strains of the parasite and also in relation to the environmental factors affecting both host and parasite and the host-parasite complex.

Where then should we concentrate our renewed attack upon this general problem? It appears rather probable that the obligate parasites are not mutating rapidly and therefore the securing of resistant varieties is somewhat of a permanent advance. The opposite situation is more probable with the less highly specialized parasites, so it would appear most desirable to begin with the diseases caused by this group of organisms. An added incentive in the same direction arises from the hope that such less-specialized diseases may yield their secrets somewhat more readily and thus form a basis for the more difficult problems of the obligate parasitic diseases. The greater ease of manipulating the infective material also favors this approach.

The tendency of an invading organism is apparently toward chemical antagonism, killing of the host, and the use of the nonliving organic remains. The facultative organisms often accomplish this, while the obligate parasites fall short. Why? The

flecking of the highly resistant wheat plants by the invading rust and the death of the invading organism indicate a toxic host action rather than a lack of food for the fungus. A similar conclusion appears to be true as regards the potato strains resistant to the wart disease. Are parasitism and resistance reciprocals? There has been a rather strong feeling that if it could be known why a fungus invades the host, we would be well toward the solution of resistance. Thus Massee ('25) believed that the presence of attractive substances in the host causes chemotropic stimulation of the fungus and that this accounts for parasitism. The lack of these attractive chemical substances would cause resistance. However, may not the parasitism of the rust on wheat be due to the presence of transitory food factors, while the resistance of certain varieties be due to the presence of toxic material? Massee failed to educate certain fungi to become parasites, yet succeeded with others, indicating possible materials in plants which are toxic to some fungi and not to others. Obligate parasites may possibly require specific, labile substances in the host to which they have become specifically bound. This could hardly be true in the alternative type of disease in which the pathogene usually grows exceedingly well on a great variety of media. In this latter type, therefore, if resistance is due to a biochemical factor it is more likely concerned with the presence of toxic materials than with the absence of food factors.

The wide distribution of certain classes of specialized products in the plant kingdom, many of which are toxic to fungi, suggests strongly that resistance may often be associated with the relative abundance of one or more such substances. This would accord well with the fact that most kinds of resistance are relative in amount and vary with different varieties of the same host. Several workers have clearly demonstrated the toxic effects of tannins and of certain organic acids, alkaloids, and glucosides upon fungi. Walker ('29) and his co-workers (Link, Dickson and Walker, '29; Angell, Walker and Link, '30) seem to have definitely demonstrated that the presence of protocatechuic acid in the outer scales of the red and yellow onions is the cause of resistance of these varieties to the onion smudge disease. It is important then to study a definite fungus in relation to the special

chemical products of the hosts upon which it grows naturally or by artificial inoculation. It is clear that we must know much more of the specific compounds produced by plants rather than be satisfied with routine analyses for carbohydrates, total nitrogen, and the like. That resistance is in certain cases associated with chemical materials is indicated in many ways. It is reported that injection of malic, tartaric, and citric acids into the roots of apple trees made them immune to certain diseases. Apple and peach stocks were made resistant to *Oidium farinosum* and *Exoascus deformans* by the grafting in of resistant wild scions. The toxic action of certain plant juices to fungi of parasitic habit as described later on indicates the same conclusion.

It is possible that in certain cases the resistant quality is effective against several diseases of a similar type, although caused by fungi of diverse relationships. Vavilov ('14) cites *Triticum monococcum* as being immune to brown and yellow rusts and stinking smut, and resistant to the powdery mildew. *Triticum durum* and *T. polonicum* likewise are resistant to both brown and yellow rust and mildew. Conversely, diseases of different types may show no similarity in their lists of resistant varieties. Thus Italian clovers are susceptible to anthracnose and resistant to mildew, while some American strains are resistant to anthracnose and very susceptible to mildew (Monteith, '24).

Data on resistant varieties need very careful analysis, since even in the same disease and on the same host there may be two or more interacting causes of resistance, i. e., some physiologic, some morphologic, and some environmental, or combinations of these. Evidence of this is seen in the lack of complete agreement in the results from greenhouse and field experiments upon resistant varieties. The observation that black stem rust of wheat grows only in the chlorenchymatous collenchyma tissue and not in the sclerenchyma (Hursh, '24), together with many other observations on probable chemical influences, indicates the complex nature of certain kinds of resistance. Genetical studies also show that while some resistance apparently is due to a simple factor, in other cases there are multiple factors concerned.

From some experiments reported by Vavilov ('14) it appears probable that within the same species the cause of resistance may

vary with the different varieties of host in relation to the same disease. A Persian wheat was found immune to the powdery mildew, *Erysiphe graminis*. Other varieties of wheat are also at least highly resistant to the same disease, yet crosses of Persian on susceptible varieties gave immune F_1 plants, while other resistant varieties crossed on susceptible ones gave susceptible plants in the hybrid generation.

From the examples referred to in this discussion it appears that when viewed as a whole the subject of disease resistance is exceedingly complicated. However, a careful analysis of the various factors involved in any given disease followed by experiments planned to test these, one at a time, will make it possible to approach closely a solution of the problem. In a similar manner the various fundamental physiological bases of pathological phenomena can be attacked and definite progress made. These advances can hardly be made as a mere incident to routine pathological studies, but must be a major project of experimentation.

We may summarize, as follows, the preceding discussion:

1. A careful collation of past observations is needed, taking care that they shall be checked by recent results and by the results in contributing fields of investigation.

2. There should be a clearer recognition of possible types of resistance as based upon the various types of parasitism, though the causes of these two phenomena may not be related.

3. The environmental effects upon disease should be analyzed as far as possible into the effects upon the host, upon the parasite, and upon the host-parasite complex.

4. An open mind should be kept toward the probability that there is no general explanation for parasitism or for resistance, but rather a specific one for each disease which may involve several factors or only one.

5. Close coöperation among biochemists, physiologists, and pathologists is most urgent.

6. Special attention must be given to the individual, characteristic chemical products of each plant studied, as related to their toxicity to the disease-producing organisms which occur on that host.

7. The study of the fundamental problems in pathology should be treated as a special field of inquiry worthy of attention in its own right and not simply as an adjunct to the study of methods of combating disease.

Considerations such as have just been discussed have led to a project for the study of some of the biochemical relationships of certain disease-producing fungi and their host plants. Some investigations in this field are reported in the following sections.

II. The Glucoside Content of Flax

During a study (Reynolds, '26) of the nutritional relations of *Fusarium lini*, which is the causal agent of the wilt disease of flax, it was found that extracts of flax are poisonous to this fungus. This toxic quality was manifest in Fermi's medium which is a relatively poor one for the growth of *Fusarium lini*. It also appeared that an extract from a strain of flax which resisted the parasitic attack of this fungus was more toxic than one from a non-resistant flax. It was suggested that the hydrocyanic glucoside of flax might be the cause of this toxic quality since *Fusarium lini* is very sensitive to the presence of hydrocyanic acid in culture media (Reynolds, '24). It seemed desirable therefore to determine as accurately as possible the quantitative occurrence of this glucoside and to study further the toxic nature of flax.

Numerous more or less complicated methods of estimating the quantity of hydrocyanic acid produced by plant materials have been described and tested. None of these seemed satisfactory, since the purposes of the estimations and the nature of the plant materials were different from those of the proposed study. In the present investigation it was desired to make use of the flax material, after the estimation for fungous culture studies, with as little change in its characteristics as possible, and hence it was decided to use the Roe aeration method of extraction (Roe, '23, '24) modified as might become necessary.

The best procedure followed was to grind the green or dry flax material, add a definite proportion of water, and let it stand over night. This allows time for the specific enzyme, linase (Armstrong and Eyre, '12; Eyre, '12), which is in the flax, to hydrolyze the glucoside into HCN, glucose, and acetone. In order to get a

thorough mixing of the plant material and a complete aeration during the process of extraction, a gas-tight, motor-driven stirrer modified from one described by Hiers ('26) was used and fitted into the flask containing the flax mash, as soon as possible after the grinding. A preliminary freezing of the green flax and grinding in the refrigeration room at a temperature below the freezing point of water further conserved the HCN by preventing enzyme action until the water had been added and the stirrer put in place. The aeration was accomplished by a slow evacuation of the stirrer-flask, thus pulling a stream of air through an inlet tube opening well below the surface of the mash, and bubbling it out into a train of three gas washing bottles made up with Folin's ammonia tubes and containing a 5 per cent potassium hydroxide solution (fig. 1). The hydrocyanic acid, being very volatile, readily passed with the air into the hydroxide where it was changed into a weak potassium cyanide. Only rarely was any cyanide discovered in the third bottle of the train. By titrating this alkaline-potassium cyanide solution with a standard one hundredth molar silver nitrate in a manner somewhat similar to that recently reported by Bishop ('27), it was possible to get a very accurate determination of the amount of HCN caught in the hydroxide. For each experiment the percentage dry weight of each strain of flax was determined and the HCN content calculated in terms of the dry weight of the material used in the estimation. Numerous precautions and tests, unnecessary to detail here, were used in order to insure comparable results in the same experiment. While not all of the glucoside present in the flax could be determined in the HCN thus evolved, estimations run directly in comparison with one another under identical conditions and upon identical materials (Exps. 69 & 70) showed that such a method gave excellent checks.

Seven different strains of flax supplied by Professor H. L. Bolley of the North Dakota Agricultural Experiment Station and selected by him for different degrees of resistance to the flax wilt disease were used. Professor Bolley's designation of the relative resistance of these seven strains of flax is as follows:

1—NDR 114—Very resistant.

2—NDR 119 (Buda)—Very resistant.

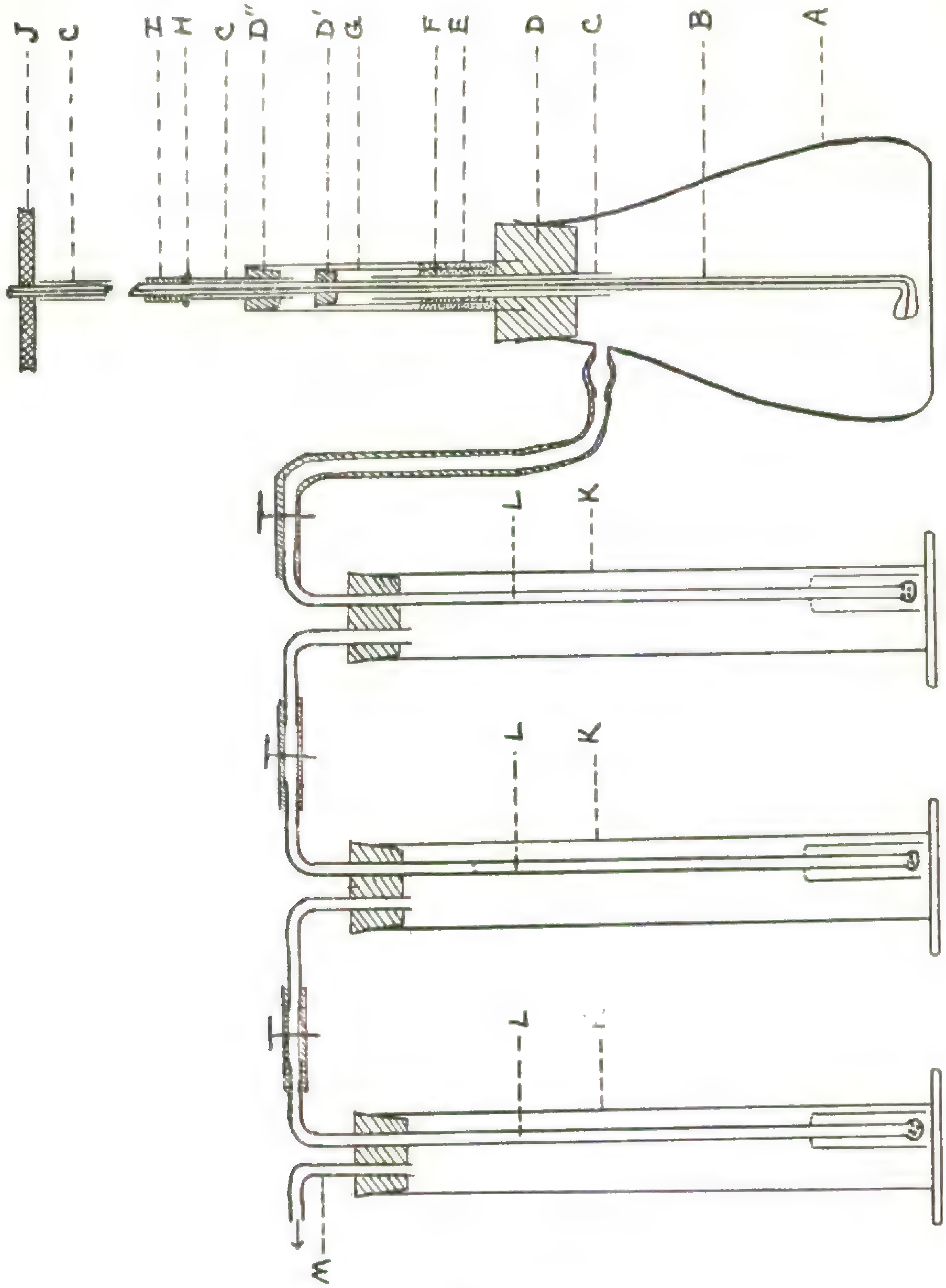


Fig. 1. Key to symbols.

A—One liter, or 500-cc., wide-mouth, side-neck, pyrex flask, with ground flax material in water.
B—Heavy-walled, glass tubing, 7 mm. o. d., bent into a paddle and with the bore left open at both ends. Air enters at the top.
C—Bearing tubes of 8 mm. i. d. with heavy grease as lubricant.
D, D′, D″—Rubber stoppers, # 7 or # 8, # 0, and # 3 or # 4, respectively.
E—Tube 23 mm. by 140 mm. Lower end buried in D.
F—Mercury seal.
G—Tube 16 mm. by 80 mm.
H—Loose metal washer.
I—Heavy-walled rubber tubing.
J—Wooden or cork pulley.
K—Cylinders with 5 per cent KOH solution.
L—Folin ammonia absorption tubes.
M—Attachment for suction.

3—L-79—Good resistance.

4—Cross—Breaking up—Fair wilt resistance.

5—Cross—Fairly good resistance.

6—N.D. 155—Tall fiber—large seed. No resistance on our sick plots.

7—N.D. 1215—No resistance under our conditions.

Different ages of flax and different environmental conditions of growth were also tested in an effort to determine their effects upon the amount of glucoside produced. The HCN in whole plants and in roots and shoots separated was also determined. In all, 66 separate estimations were carried out, besides a considerable number of preliminary and partial tests. The numerical data for all these determinations are given in table I. The percentage of HCN is calculated on the basis of the dry weight of the flax material. From .2 to .3 per cent HCN, corresponding to about 2 to 3 per cent glucoside, is a very high content, while about 1 per cent glucoside is a normally high content. Less than .1 per cent glucoside is a very low quantity for this series of experiments, except in fully matured flax which has almost none.

The following table gives a series of analyses made in England by Dunstan, Henry and Auld ('06), which illustrates the usual rise and fall of glucoside content in the flax plant from seed to seed. These are minimum quantities, since the method of analysis does not fully conserve the hydrocyanic acid present in the plants, and there are evidences from the experiments reported in the present paper that the glucoside content of some of the strains tested is considerably higher than shown in table II.

Since the experiments reported here were often designed to test the effect of age, environmental conditions, and various methods of determining the cyanogen content, it is evident that in most cases the numerical data from different experiments are not directly comparable. Two or more strains of flax, listed under the same experiment number and of the same age, were generally handled in a similar fashion and the data are usually comparable. It appears from a consideration of all this data that the quantity of HCN which can be evolved from the plant material is strongly influenced by the environmental conditions which have surrounded the growing plants and that a change of such conditions

TABLE I

SUMMARY OF HCN DETERMINATIONS

Exp. No.	Flax No.	Height (inches)	Age	Per cent HCN in flax strain Number								Notes
				1	2	3	4	5	6	7	11	
29	1		6½ wks.	.18								
31	7		7 wks.							.12		Shoots
										.07		Roots
33	4	5½–6	8 wks.				.12					Whole plants
34	2	7½–8½	8 wks.		.11							Whole plants
37	6	5½–6	8 wks.						.097			Whole plants
40	1	2½	5½ wks.	.12								High dry weight. Whole
42	6	4	6 wks.						.066			Whole plants
42	5	5½–6	6 wks.					.08				Whole plants
42	3	3½–4½	6 wks.			.075						Whole plants
42	2	4½–5	6 wks.		.085							Whole plants
43	2	3–3½	2 wks.		.083							Constant-light room
43	6	3–4	2 wks.						.11			Constant-light room
57	3	10–11	11 wks.			.045						
		7½–8				.078						From same flat
60	1	10–11	11 wks.	.20								Tops, 2–4 inches
61	1	Seedlings	5 days	.28								Stems. In dark
				.15								Roots. In dark
62	2	3–3½	15 days		.054							Constant light. Poorly watered.
		(2–6½)										Irregular height
62	6	4(2–7)	15 days						.046			Constant light. Poorly watered.
												Irregular height
64	6	10–14	8 wks.						.086			Low-temp. house, 52° C. night
64	6	7–11	8 wks.						.094			High-temp. house, 78° C.
66	2	10–14	8 wks.		.061							Low-temp. house
66	2	7–11	8 wks.		.069							High-temp. house
68	1	8½–10	6½ wks.	.031								Low-temp. house
68	2	8–9½	6½ wks.		.085							Low-temp. house
69	1	9½–12	7 wks.	.022								
				.020								Checks
70	7	4–4½	3 wks.							.127		
										.131		Checks
73	3	4–5½	3 wks.			.059						
74	2	6–9	16 days		.087							Constant light
74	6	7½–9½	16 days						.19			Plus 2 days ordinary
75	2	Seedlings	5 days		.35							Stems by aeration
					.062							Roots by aeration

TABLE I (*continued*)

Exp. No.	Flax No.	Height (inches)	Age	Per cent HCN in flax strain Number								Notes
				1	2	3	4	5	6	7	11	
76	2	Seedlings	5 days		.31							Stems }Juice filtered into KOH
					.051							Roots }
77	4	3½–4½	3 wks.				.11					59° C. at night
	6	3½–4½							.089			
79	2	3–4	16 days		.19							
82	2	7–8	30 days		.053							
	6	7½							.06			
83	1	1½–2	3 wks.	.08								Aeration faulty
83	4	1½	3 wks.				.13					
85	2	4–5	19 days		.18							
	5	4½–5½						.061				
87	1	3–4	30 days	.034								Slow-growing in cold-frame
	1	20–22	7–8 wks.	Trace								
90	4	3–5	5 wks.				.073					
91	1	2½–3	3 wks.	.015								
	6	2½–3							.011			In cold-frame
99	1	4½–5	4 wks.	.066								
	6	3–4	4 wks.						.056			In cold-frame
100	1	6–8	6 wks.	.019								In cold-frame
104	4	7½–9	6 wks.				.029					
108	2a	5–6	5 wks.		.063							Healthy
		3–4			.0083							Yellow
109	6	4½–6	5 wks.						.078			
112	1	4½–6½	7 wks.	.017								
	3	5–6				.009						
113	1	5–7	7 wks.	.006								Duplication of No. 112 but 2 days later
	3	6–7	& 2 days			.01						
114	2a	6½–11	7 wks.		.01							
	6	6½–8							.012			
125	2a	Seedlings			.094							Possible loss during storage
	7a	Seedlings								.027		
128	11	2–4	2 wks.								.243	
136	1a	3–3½	12 days	.11								
145	11	5–10	5–6 wks.								.20	

Note:—Nos. 1a and 2a a different year's production of seed; No. 11 a highly resistant selection from No. 1.

TABLE II

THE GENERAL COURSE OF HCN CONTENT OF FLAX THROUGHOUT THE LIFE OF THE PLANT

Height of flax plant in inches	Per cent HCN found	Per cent glucoside calculated
Seed	0.008	0.07
1–1.5	.15	1.4
2–3	.17	1.5
3–4	.15	1.4
4–5	.13	1.2
5–6	.10	0.9
6–7	.10	0.9
8–9	.08	0.7
12–15	.07	0.6
15–18	.03	0.3
18	0.009	0.08
18	None	None

for even a day or so may influence this quantitative characteristic immediately (Exps. 112 and 113). Willaman and West ('16) noted some climatic effect on the production of HCN by sorghum, although they were inclined to believe that varietal constitution caused greater modifications than did climatic differences. Pinckney ('24), however, was convinced that HCN was increased in direct proportion to the increase of nitrate fertilizer on a low nitrate field, and that yellowish sorghum produced little if any HCN when the green plants contained a good supply.

While in general young flax runs high in hydrocyanic glucoside and old flax low, yet it appears that neither age nor height as such are proper indicators of the probable HCN production. The condition which seems to influence this quantitative factor is the number of actively functioning cells. Thus plants of the same age, but of different physiologic vigor, may develop nearly eight times as much HCN in the normal healthy specimens as in yellow retarded ones (Exp. 108). Experiments 43 and 62, although originally intended to be duplicates, carried on in the constant-light room, do not show the same quantities of HCN. In the latter experiment, due to the crowded condition of the room, the flax flats were irregularly and inadequately watered. The resulting plants, although of equal age, were very unequal in size and vigor of growth. The amounts of HCN in both strains were noticeably less than in Experiment 43 in which the growth was

uniform and normal. In the examples cited the irregular watering of the flats seemed to be the factor which largely determined the relative vigor of the plants. The upper two to four inches of flax eleven weeks old, which was in vigorous physiologic condition, gave a high quantity of HCN hardly equalled even by very young flax (Exp. 60). Thus it would appear that the reason the percentage of HCN in flax shows a steady decrease from a maximum at 2–4 inches high is because a continually decreasing proportion of the plant is composed of actively functioning cells.

Temperature variations of medium range did not seem to modify the glucoside content (Exp. 64 and 66). The use of the constant-light room did not seem to cause any special change in the quantity either, although the life cycle was greatly shortened so that seed was matured in about half the usual time. The shoots of flax seedlings may contain five times as much glucoside as the roots (Exps. 75 and 76), while in older plants there is a smaller difference (Exp. 31), due mainly perhaps to the drop in the percentage in the shoot. In the older plants it is very difficult to get the smaller and hence physiologically more active roots for a quantitative determination, so that it is not known at present how much glucoside is in the whole root system. It is interesting to note that while fully mature flax seed contains very little, if any, glucoside which may be converted into HCN, five-day-old seedlings, which had developed in the dark, had the highest percentage of the acid which was found in this series of experiments (Exps. 61, 75, and 76).

The flax strains numbered 1, 2, 3 and 4 are, in the main, strongly resistant to the wilt disease, while No. 5 is intermediate and Nos. 6 and 7 are only slightly, if at all, resistant, as determined through field tests by Professor Bolley. Although in many of the analyses the more resistant varieties ran high in glucoside content and the less resistant ones low (table III) not enough data were gathered to prove definitely a correlation (Exps. 42, 77, 85, etc.). It may be noted from table III that the 2–6 pair, which in four out of seven tests showed a greater amount of HCN in the susceptible flax than in the resistant, accounts for four out of the nine cases in which this same relationship is seen. Under most conditions the No. 6 flax seems to produce more HCN than No. 2.

It may be that it has more glucoside or that under certain circumstances it produces a larger amount of linase, or a more active enzyme. Strain 4 consistently developed a high quantity of HCN for the conditions under which it was growing and constitutes the other apparent exception to a correlation between strong resistance and high glucoside content. However, Professor Bolley's characterization of its degree of resistance indicates that it is rather likely to be exceptional.

TABLE III

PAIRS OF FLAX VARIETIES COMPARED AS TO RELATIVE QUANTITIES OF HCN. R = MORE RESISTANT MEMBER OF PAIR; S = MORE SUSCEPTIBLE

Exp. No.	Pairs of varieties	R more HCN than S	S more HCN than R
42	5-6	*	
	2-3	*	
	2-6	*	
	3-6	*	
	3-5		*
	2-5	*	
43	2-6		*
62	2-6	*	
68	1-2		*
74	2-6		*
77	4-6	*	
82	2-6		*
83	1-4		*
85	2-5	*	
91	1-6	*	
99	1-6	*	
100, 104	1-4		*
112	1-3	*	
113	1-3		*
114	2-6		*
125	2-6	*	

It is evident from Broadfoot's work ('26) that each of the different strains of flax is resistant to the different strains of *Fusarium lini* in different degrees. Because of these considerations and of the variety of conditions surrounding the plants and the ease with which the glucoside content may change we must conclude that the lack of an evident, exact correlation does not disprove a possible causal relationship between resistance and glucoside production. Many more determinations of the glucoside and of the changes in amounts of linase in flax must be made before a clear

picture of the distribution and significance of HCN can be drawn. Such a study is planned for the near future.

While it had been determined formerly (Reynolds, '24) that potassium cyanide inhibits the growth of *Fusarium lini* on agar plates at a concentration of about .03M it was thought best to test the effect of cyanide in liquid cultures. The following experiment (No. 15) was made: A solution of hydrocyanic acid was prepared so that 5.2 cc. in a 50-cc. culture would give a .03M concentration of HCN. The standard culture medium described in the third section of the paper was used and a series of cultures made as indicated in table IV. Some of these were inoculated with No. 2 *Fusarium lini* and some with No. 7 *Fusarium lini*. The former was one of Broadfoot's ('26) most virulent flax parasites and the latter one of the least parasitic of his group. The cultures in the Florence flasks (F) were sealed with paraffin to

TABLE IV

EFFECT OF CYANIDE IN LIQUID CULTURES

F. lini culture	Amount of HCN sol. (cc.)	Style of flask	Average growth in milligrams of dry weight at		
			15° C.	20° C.	27° C.
# 2	0.2	F	*3—(4)	3—188.8	3—122.0
# 7	0.2	F	3—229.7	3—347.6	3—233.9
# 2	1.0	F	3—(6)	3—143.3	3— 90.0
# 7	1.0	F	3—(1)	3—188.7	3—(2)
# 2	5.2	F	2—none	2—none	3—none
# 7	5.2	F	1—none	3—none	3—none
# 2	1.0	E	2—(5)	2— 48.0	2— 75.1
# 7	1.0	E	1—Trace	2—222.3	2—300.7
# 2	5.20	E	2—none	2—(7)	2— 36.6
# 7	5.20	E	2—none	2—(7)	2—(3)
# 2	None	E		3—222.9	
# 2	None	F		3—266.1	2— 89.9
# 7	None	F	2—343.4	2—260.2	
# 7	None	E	3—220.7		

* The number preceding the dash indicates the number of cultures in the set. A number in parentheses refers to the following notes.

Notes:

(1) Two with possibly a trace of growth, and third no growth.
(2) One with undetermined amount of growth; one, trace; one, none.
(3) One culture, 31.4 mg.; one, trace.
(4) One culture, 33.9 mg.; one, 7 mg.; one with undetermined amount.
(5) One culture, 30.3 mg.; one, trace around inoculum.
(6) One culture, 21.4 mg.; two, undetermined amounts.
(7) One culture, trace; one, none.

prevent, as far as possible, the escape of HCN. The Erlenmeyer flasks (E) were closed only with cotton plugs.

It will be seen from the results tabulated that the greatest concentration of HCN is practically always completely inhibitive except at the higher temperatures in the non-sealed flasks. The irregular results here indicate that enough of the HCN was lost by diffusion into the air to reduce slightly the toxic quality. This is indicated somewhat also by the observation that nearly all of the HCN flasks in the 27° C. incubator which showed growth were on the lower shelf nearest the heating unit. It appears that the fungus was less resistant to the toxic effect of the HCN at 15° C. than at 20° C., as one would expect from the fact that the former temperature is not as favorable for this species as the latter. The irregular numerical results, especially of the higher concentrations, are characteristic of cultures which are near the inhibitive, toxic concentration of poisons. The No. 2 strain of *F. lini* is a less vigorous grower in this standard medium than the No. 7 strain, but it would seem that there is little difference between the two under the action of the HCN in culture.

The results of the analyses given in table I show that in the older flax roots the proportion of HCN to dry weight is much lower than in the shoot. However, they also indicate that in young roots, as found in seedlings, the percentage of HCN may rise to a considerable amount. It is stated by Armstrong and Armstrong ('10) that the entrance of certain substances into a plant which has a cyanogenetic glucoside causes a "cumulative" change, so that a very small portion of the substance produces a large relative production of HCN. If this is true it is entirely conceivable that the entrance of a fungus might likewise stimulate a concentration of the glucoside at the point of attack. Hence the normal concentration of HCN, as determined by analyses such as reported here, does not necessarily have to indicate a toxic concentration in order to account for resistance.

While the various experimental evidences and the considerations just discussed do not give positive proof either for or against the causal relationship between the presence of the cyanophoric glucoside in flax and a certain varietal resistance to the wilt disease, yet it would seem that at least a part of the resistant

quality may be attributed to this chemical condition. In view, however, of the experiments reported in the third section of this paper it is probable that other toxic conditions exist in flax which may also be related to resistance.

III. Flax Extracts Toxic to Fungi

Although it had been demonstrated that under certain conditions flax extracts retarded the growth of *Fusarium lini* in culture (Reynolds, '24), it was desired to determine what concentration, if any, might prevent the growth of the fungus. Furthermore, as stated in the foregoing section, it was desired to study the effect of the cyanide content of flax upon the fungous growth. Hence water extracts of both fresh and dried flax were tested as regards toxicity to *Fusarium lini*. These extracts were made by grinding the flax and steeping it in water, usually over night. Various methods of filtering and the effects of these upon the toxic quality of the extracts were tested. None of these methods used prevented the characteristic toxic effects. To the filtered liquid were added salts and glucose in the same proportions as used in the standard check medium (A) throughout this study. The formula for this was water 1000 cc., magnesium sulphate 2 grams, later reduced to 1 gram, calcium acid phosphate 1 gram, potassium nitrate 10 grams, and dextrose 20 grams. A portion of each flax extract thus provided with standard quantities of nutrients was autoclaved at 15–20 pounds pressure for twenty minutes; and a corresponding portion filtered through bacteriological filters. At first the Berkefeld and Mandler filter cylinders were used, but the Seitz filter was later adopted for speed and convenience. Sterilized pipettes and culture chambers provided means of transferring the sterilized medium when necessary.

Through the kindness of Dr. E. C. Stakman seven of the strains of *Fusarium lini* with which Broadfoot ('26) carried on his experiments were made available. These were kept in culture and used during the course of the work. They were numbered from 2 to 8 approximately in their general decreasing order of pathogenicity, although it is clear that when several strains of flax are tested the flax strains and those of the fungus can not be arranged in a simple series in relation to one another. Those having the

higher numbers, especially 7 and 8, grew more abundantly in culture media than those having the lower numbers. Many hundreds of cultures were made and the dry weight of growth produced in fourteen days was determined. In nearly all cases identical triplicate cultures were run and averaged for the dry weights. Checks on the standard medium were carried with each set of new inoculations. Flax extracts were made from nearly all of the flax varieties and conditions of growth which were tested for hydrocyanic acid as reported in the preceding section. At the same time that each strain of flax was being tested for HCN content, culture series were run, using both fresh extracts and the extract which had been aerated and hence deprived of most of the HCN. The percentage dry weight of each sample of flax was determined before it was used in the HCN and culture studies. This was necessary since different ages and conditions of growth were being tested. In the course of the aeration process foaming sometimes took place, and at different times diphenyl ether, amyl alcohol, and caprylic alcohol were used to break the foam. Each of these was tested a number of times in different ways as to its effect on the quantity of growth of the fungus. Neither amyl alcohol nor diphenyl ether showed any repressive effect on the fungus and the very dilute quantities used did not stimulate growth. Caprylic alcohol proved to be extremely toxic so that one or two drops in a 50-cc. culture prevented growth completely.

In table v a summary of a considerable number of representative experiments is given. The standard concentration of flax extract was 9 parts water to 1 part dry weight of flax. From .2 to .3 of a gram was the usual dry weight of mycelium produced in the standard check medium A. It was soon evident that dilute flax extracts, that is, below one-half standard strength prepared as stated above, usually stimulated the growth of this *Fusarium*. From .3 to .5 of a gram of growth was usual and the higher the concentration of flax extract, up to certain limits, the greater was the mycelial growth. This favorable effect of the flax medium can probably be ascribed to the added nutritive materials from the flax. Fresh, green flax and dry flax powder

TABLE V

RESULTS OF CULTIVATION OF F. LINI IN FLAX EXTRACTS

Exp. No.	Flax No. and height in inches	Concentration	Filtered (F) Autoclaved (A)	Previous treatment	Result	Remarks
B # 1	# 6—3½	1	A	Powdered	O	Shoot*
B # 1	# 6—3½	1/4–1/2	A	Powdered	<	Shoot
B # 1	# 6—3½	1/2–1	F	Powdered	O	Shoot
B # 1	# 6—3½	1/4–1/2	F	Powdered	< S	Shoot
B # 2	# 2a—2½	1/4–1	A	Powdered	<	Entire
B # 2	# 2a—2½	1/4–1	F	Powdered	<	Entire
B # 3	# 7—7	1/4–1	A	Powdered	<	Entire
B # 3	# 7—7	5/12–1	F	Powdered	O	Entire
B # 3	# 7—7	1/4–1/3	F	Powdered	G	Entire
B # 4	# 5—12	1/4–1	A	Powdered	G	Leaves
B # 5	# 5—12	1/4–1	A	Powdered	G	Stems
B # 6	# 11—6	1	A	Powdered	O	Leaves
B # 6	# 11—6	1/4–1/2	A	Powdered	G	Leaves
B # 6	# 11—6	1/4–1	F. A.	Powdered	G	Leaves
B # 7	# 11—6	1/4–1	F. A.	Powdered	G	Stems
17	# 2—2	00	F	Powdered	G >	Roots
18	# 3—6	1/3	F	Powdered	G	Roots
22	# 5—8	1/4	F. A.	Aerated	G	Shoot
22	# 5—8	1/20	F. A.	Aerated	G >	Shoot
22	# 6—7	1/3	F		O	Shoot
22	# 6—7	1/3	A		G	Shoot
22	# 6—7	1/12	F		G	Shoot
22	# 6—7	1/12	A		G>	Shoot
30	# 1	1/8	F	Aerated	G	Shoot
35	# 7	1/10	F	Aerated	G	Shoot
36	# 4—6	1/8	F. A.	Aerated	G	Whole
38	# 6—6	1/20	F	Aerated	G	Less than in Exp. 36
39	# 2—8	1/16	F. A.	Aerated	G	
41	# 1—2½	1/14	F. A.	Aerated	G	
53	# 6	1/7 & 1/28	F		G	Fresh, green
54	# 2	1/7 & 1/28	F. A.	Aerated	G	Fresh, green
54	# 6	1/6 & 1/24	F. A.	Aerated	G	Fresh, green
58	# 3—7½	1/10–1/40	F		G-M	Fresh, green
58	# 3—10	1/15–1/60	F		G-M	Fresh, green
63	# 6—10	1/10–1/20	F. A.		G >	Fresh, green
65	# 2—10	1/8–1/16	F. A.		G >	Fresh, green
67	# 1 & 2—8	1/17	F. A.		G	Fresh, green
71	# 7—4	1/14	F. A.		G-M-S	Fresh, green
72	# 3—4	1/10–1/20	F. A.		G	Fresh, green
78	# 4 & 6—4	1/16–1/32	F. A.		G	Fresh, green
80	# 2—4	1/10–1/20	F. A.		G	Fresh, green
81	# 2 & 7	2, 1, 1/2	F. A.		O-G	Fresh, green
84	# 1 & 4–1½	1/5	F. A.		G	Fresh, green
86	# 2 & 5—5	1/4	F. A.		G	Fresh, green
88	# 1—3 & 20		F. A.		G	Fresh, green
92	# 1 & 6—3	1/4 & 1/7	F		G	Fresh, green
95	# 2 & 7	2, 1, 1/2	F. A.		O	
98	# 1 & 6—4	1/3–1/6	F. A.		G	Fresh, green
101	# 7—10	2/3–1/3	F. A.		G >	Roots & shoots separate

TABLE V (*continued*)

Exp. No.	Flax No. and height in inches	Concentration	Filtered (F) Autoclaved (A)	Previous treatment	Result	Remarks
117	# 11—10	1	F		G	Dry roots only
121	# 4—	1	F		O	Dried flax powder
123	# 1a—3	1	F		O	Fresh, green flax
127	# 4—	1	F		O	Dry, powdered

*—Unless definitely stated the extract was made from powdered flax.
M—About equal to growth on Med. A.
O—No growth of fungus developed.
S—Small growth, less than on checks in Med. A.
G—Good growth, distinctly better than checks on Med. A.
>—Weight of fungus decreasing with dilution of extract.
OO—Diluted 50–100 times.
<—Weight of fungus increasing with dilution of extract.

have both been used in preparing these extracts, as illustrated in the following tabulations of results from a few experiments.

Experiment 71—73.2 gms. # 7 fresh green flax to 1000 cc. water

	Filtered		Autoclaved	
	# 2 *F. lini*	# 7 *F. lini*	# 2 *F. lini*	# 7 *F. lini*
Full str. extr.	.2975	.3707	.2160	.3619
Half str. extr.	.2286	.2354	.2716	.3482
Checks # 71 & # 72	.2442	.2885		

Experiment 72—106.5 gms. # 3 fresh green flax to 1000 cc. water

Full str. extr.	.3147 (.0705)*	.3931 (.1046)	.2977 (.0535)	.3697 (.0812)
Half str. extr.	.2782 (.0340)	.3323 (.0438)	.2814 (.0372)	.3302 (.0417)

* The numbers in parentheses show increase in growth in flax extract over the growth in the check medium.

Experiment 78—61.45 gms. # 4 fresh green flax to 1000 cc. water

Full str. extr.	.2832	.3160	.2569	.3079
Half str. extr.	.2687	.3043	.2579	.2905

77.14 gms. # 6 fresh green flax to 1000 cc. water

Full str. extr.	.3045	.3323	.2973	.3318
Half str. extr.	.2704	.2871*	.2665	.3017
Checks	.2179	.2218		

* Had been contaminated and refiltered before inoculation.

Experiment 80—94 gms. # 2 fresh green flax to 1000 cc. water

Full str. extr.	.2771	.3033	.2850	.3048
Half str. extr.	.2973	.2623	.2799	.2817
Checks	.2179	.2218		

Experiment 81—102.0479 gms. air-dry # 2 flax powder to 500 cc. water. 102.2809 gms. air-dry # 7 flax powder to 500 cc. water. # 7 *F. lini* used

	# 2 Flax	# 7 Flax	# 2 Flax	# 7 Flax
Full str.	.0000	.0000	.0000	.0000
Half str.	.0000	.0000	.0000	.0000
Quarter str.	.5013	.5149	.5041	.5156
Checks	.2409			

The first four experiments tabulated are typical of many which were carried concurrently with those in which the determinations of cyanide content were made. It will be noted that # 2 *F. lini* consistently produced less growth than # 7 on all flax extracts and the check medium. In Experiment 72 a difference in growth between the check cultures and the flax extract cultures shows that the # 2 *F. lini* made less increase of growth than did # 7 *F. lini*. This would indicate that the former strain can make less use of the added nutritives from the flax or else is retarded more by the flax extract than the latter. It seems that the first alternative is more probable since the # 2 *F. lini* does not make as good use of the nutritives in the check medium as does # 7, and at these concentrations of flax extract a retarding action is not evident. Autoclaving seems to have little effect in changing the nutritive qualities of the flax media at these concentrations, for the differences between the growth in the autoclaved and the filtered media are neither great nor regular. In Experiment 80, since there is more flax per liter than in Experiments 71 and 78,

we should expect a larger fungous growth. However, in the main this is not true. It is possible that a slight toxic effect is exhibited here, but certainly the figures are not clearly significant. Experiment 81, however, exhibits a clear case of toxicity for the half- and full-strength flax cultures and as clearly indicates that the quarter strength is more than twice as effective as the check medium in producing growth. This latter concentration corresponds with the half-standard strength. The juice expressed from fresh flax, when used as above without dilution, also prevented growth of the fungus. In different varieties of flax it was found that various concentrations prevented the growth of *F. lini*. It was necessary therefore to attempt to determine the minimum concentration of flax extracts of different varieties which would just prevent growth of the fungus.

Experiment 147 will illustrate the procedure. Dry flax powder (# 3 flax), weighing 25.34 gms., was steeped with 100 cc. of distilled water for two days. The liquid was pressed out and more water added with successive pressings until 250 cc. of flax extract had been obtained. Since a small meat press was used some water was left in the flax material and the total water added was somewhat more than the 90 per cent, which has been used as the arbitrary standard. The salts and glucose were dissolved in the standard proportions and the medium was then filtered through the Seitz bacteriological filter. With sterile, graduated pipettes a series of cultures was made as follows, and designated "Series A":—Three tubes of Check Medium A, marked O; three tubes of full-strength extract, marked 1; three tubes with 9 cc. of extract, and 3 cc. of Medium A, marked ¾; three tubes with 6 cc. of extract and 6 cc. of Medium A, marked ½; and three tubes with 3 cc. of extract and 9 cc. of Medium A, marked ¼. These were left several days in the incubator to test for freedom from contamination and then inoculated with # 7 *Fusarium lini*. Six days after inoculation there was no growth except in the checks (0). At this time one set, from 0–¼, was reinoculated and designated as X. A second set was filtered into fresh tubes, autoclaved, inoculated, and designated Y. A set Z, made up as follows from the third tube of full-strength flax extract of the original set A, was autoclaved and inoculated:—

(1) 2.0 cc. of full-str. extract and 8.0 cc. of Medium A
(2) 1.5 cc. of full-str. extract and 8.5 cc. of Medium A
(3) 1.0 cc. of full-str. extract and 9.0 cc. of Medium A
(4) 0.8 cc. of full-str. extract and 9.2 cc. of Medium A
(5) 0.6 cc. of full-str. extract and 9.4 cc. of Medium A
(6) 0.4 cc. of full-str. extract and 9.6 cc. of Medium A
(7) 0.3 cc. of full-str. extract and 9.7 cc. of Medium A
(8) 0.2 cc. of full-str. extract and 9.8 cc. of Medium A
(9) 0.1 cc. of full-str. extract and 9.9 cc. of Medium A

Nine days after inoculation no fungous growth was present in sets X and Y except in the ¼-strength culture of Y, where the inoculum had become lodged at the surface of the liquid and a slight growth had developed. In set Z some growth had taken place in all the tubes with evidently much less in (1) and (2). Thus the limiting toxicity for complete inhibition was at ¼ strength for the autoclaved material, although a retarding action was manifested in the second tube of set Z. In the filtered extract the toxic limit for complete inhibition was below the ¼ strength as seen in set X.

In Experiment 102 # 3 flax powder made up one-third standard strength prevented the growth of # 7 *F. lini*. In Experiment 121 one-half strength flax extract from # 4 flax also prevented the growth of the same strain of fungus. Full-strength and one flask of half-strength extract from # 1 flax prohibited growth of # 7 *F. lini*. In this experiment (# 123) fresh, green flax, 3–3½ inches tall, from the outdoor garden was used. Both the inhibiting strengths had a pH of 3.53. A second flask of the half-strength medium produced a growth of .5087 gms., and an average of three cultures in the quarter strength was .3816 gms. The extra-large growth in the one tube of half-strength medium suggests a toxic stimulatory action. Other occasional results of this irregular nature have been noted, especially at or near the point of complete inhibition. Thirty grams of # 4 flax powder in 300 cc. of water were used in Experiment 138, from which a series of dilutions was made as follows: 1/5, 2/5, 3/5, 4/5, 9/10, and 5/5 strength. A regular increasing gradation of growth from the 3/5 concentration downwards, a slight growth in the 4/5, and none above indicates the approximate inhibiting concentration of this material. A considerable number of the early experiments performed in eastern New York indicated a completely inhibiting toxicity of the flax extracts at or below the standard strength, as

illustrated in the summary given above. These included both extracts from dry flax powder and extracts from fresh, green flax plants. When this work was continued at the Missouri Botanical Garden it was found that some flax powders gave this same inhibiting result, while others allowed abundant growth of *Fusarium lini* at this concentration. This was true even when inoculations were made from the same fungous culture at the same time for different flax extracts. After several series of cultures had given these conflicting results a careful check was made of the sources of the various flax powders used. It was found that uniformly those powders derived from plants grown in New York gave the inhibiting action, while those from plants grown at St. Louis failed to show this degree of toxicity. This interesting phase of the problem will be studied further, when a new supply of flax powders from several climatically different regions is available.

It is evident from these experiments that different strains of flax possess the toxic quality in different proportions and that different environmental conditions surrounding the flax determine the concentration in the same strain at different times.

The effect of heat on the toxic material of flax was tested in two ways. Flax powder was autoclaved for one hour at 18 pounds pressure and used for extracts. No growth of *F. lini* occurred in this extract at standard concentration. Inhibiting flax extracts of standard concentration have been autoclaved and tested for growth of the fungus. In most experiments the fungus was still prevented from growing, but occasionally growth developed. The latter cases have been interpreted as indicating a degree of toxicity close to the margin of inhibition and a partial injury of the toxic material by autoclaving in liquid medium.

Efforts were made to eliminate the toxicity by aeration and to transfer such toxicity to Medium A by aerating flax extracts into this medium. The latter experiment was entirely negative in results and the former essentially so. Fresh, green flax of the # 11 strain was ground and aerated twice for a total of about thirty-six hours. The HCN content was .243 per cent. The residual liquid, 240 cc., was provided with the usual salts and glucose in proper proportion and used as a culture medium for # 7 *F. lini*. A retarded development took place in two filtered

cultures and no growth in the third, while the three autoclaved flasks developed a good growth. Since this medium was somewhat less than one-half standard strength it seems improbable that the aeration had any appreciable effect on its toxicity. In Experiment 102, 39 gms. of # 3 flax powder, after a preliminary steeping in water, was aerated into 160 cc. of water, to which the salts and glucose were added to convert it into a standard Medium A plus any volatile products from the flax. This was made into three 50-cc. cultures and called A. The flax filtrate of 1000 cc., obtained after the aeration, was divided into several portions. From 500 cc. of it 280 cc. were distilled into a 5 per cent KOH solution for a cyanide determination. This portion (B) was then made up to its original volume; a portion (C) was retained unchanged; and a portion (D) was diluted to half strength. All these were prepared as usual as cultures and one half of the B, C, and D flasks were autoclaved, while the other half were used as filtered material. The following were the growth results in grams from inoculation with # 7 *F. lini:*—A, .3066; B-filtered, .5220; B-autoclaved, .4339; C-filtered, no growth; C-autoclaved, .5681; D-filtered, .4515; D-autoclaved, .4588. Autoclaving again seemed to remove the toxic effect. No toxic effect was noted in the Medium A, thus indicating that no volatile toxin was present in appreciable quantity. The process of distillation, however, destroyed the toxic condition as seen by comparing B and C. The original concentration of flax extract was about one-third standard and when diluted to half strength fell well below the inhibiting concentration as seen in the D cultures. Autoclaving makes little difference in this case.

It was thought that perhaps the toxic material was a dialyzable compound. The following experiments were therefore made to test this hypothesis. For the first experiment (# 121) 47 gms. of # 4 flax powder were left in 450 cc. of water for two days and then, after filtering, washed with several portions of water and pressings in a Buechner funnel with suction until a total of 1000 cc. of filtrate were obtained. Four hundred cc. were then dialyzed through a collodion bag, made as usual in a Kjeldahl flask. An electric stirrer was fitted into the neck of the bag, by a rubber stopper, and dialysis for two days in running tap-water was

followed by one more day in running distilled water. There were 500 cc. of liquid present at the end, to which salts and glucose were added. Fifty-cc. flask cultures were made from this and also from the remainder of the flax filtrate which had not been dialyzed, using as always salts and glucose to equal their concentration in Medium A. Half of the flask cultures were autoclaved and half filtered. None of the cultures from the filtered, original filtrate produced growth; the autoclaved, filtrate cultures produced an average growth of .5923 gms.; the dialyzed, autoclaved cultures produced .2177 gms. of fungous growth; and the filtered, dialyzed cultures had an average of .2634 gms. of fungus. As this flax extract was less than half-standard strength and during the process of dialysis considerable precipitation had taken place in the bag it was thought best to check the results carefully. In Experiment 132, 26 gms. of # 6 flax powder were used, since the # 4 flax was exhausted. The dialyzing was continued with stirring for three days with a total of 260 cc. liquid left at the end. This was filtered with suction and used without dilution as a culture medium. No growth took place in the filtered series of flasks, but a belated growth of fungus did develop in two out of the three of the autoclaved series in a twenty-day period. No numerical results were taken. If dialysis removes any of the toxicity, as seemed to be the case in the first experiment, it is not rapid nor very effective as seen from the results of the second experiment. In the latter test the filtrate was of standard strength and even in the autoclaved series still showed some toxicity both by the belated development and by the development of growth in only two out of the three flasks. Further dialysis experiments are planned covering several strains and ages of flax.

The relative effects of root and shoot extracts were tested out by an experiment (# 101) as indicated in table VI.

No toxic effects are evident at the concentration used and the root extracts provided less nutriment than those from the shoot. The greater growth of # 2 *F. lini*, as compared with # 7 *F. lini*, in the shoot cultures may indicate an ability to use flax extractives to better advantage, or possibly an ability to withstand a certain toxic action which, although not sufficient to reduce the growth of # 7 *F. lini* below the check culture, nevertheless holds back this

TABLE VI

	# 7 *F. lini*		# 2 *F. lini*	
	Filtered	Autoclaved	Filtered	Autoclaved
Root				
Full str.	.5611		.5472	.6714†
Half str.	.4057	.4580*	.3957	.4773*
Shoot				
Full str.	.7793		.8591	.8675*
Half str.	.4536	.4887*		.5775*
Checks	.2427		.2357	

* Average of 2 cultures. † One culture only.

latter fungus from making as full a growth as it should. The latter conclusion would be in accordance with the conclusion reached in Experiment 81. The greater growth of # 7 *F. lini* in the check medium, although numerically not clearly significant, is in line with all of the other cultural work with this strain as compared with # 2 *F. lini*.

It is interesting to note from these various experiments that dilutions of flax extract, which are only half as concentrated as the critical concentration for complete inhibition, often not only allow development of the fungus, but actually produce a much more abundant growth than the standard, check medium. Hence it appears that it is necessary for this toxic material to be in a rather concentrated form before it can overcome the nutritive stimulation of a culture medium favorable to the fungus. The range of concentration from that which gives greatest growth to that which is completely inhibitive is often quite narrow.

That the toxic effect is not due to acidity or alkalinity of the medium is evident from two considerations. First, the flax wilt fungus is able to grow well throughout a wide pH range. Second, the flax media which prevented growth ranged mostly from a pH of 3.56 to 3.60, with the extreme at 4.06, while the standard check medium was 3.52 and the flax medium which allowed prompt and abundant growth ranged as high as 5.00 to 6.35 when ready for inoculation. Autoclaving the flax medium sometimes raised the pH as much as a point, although at other times only a few tenths. At two different times in the course of this work abundant growths

of foreign fungi were found in flax media which completely prevented the growth of *F. lini*. In each case it was one out of three identical flasks which had become infected. One of these was *Monilia sitophila* and the other an *Aspergillus*. This indicates that the toxic material in flax is at least somewhat specific for the *Fusarium*, but many further tests must be made to determine the range of toxic effect upon fungi in general and plant pathogenes in particular. A test was made to determine the effect of the toxic substance upon the fungus by transferring a mass of mycelium from a flax extract in which it had failed to grow into a flask of Medium A. There was no growth from this inoculum, showing that the flax medium had killed the fungus, both mycelium and spores, and not simply prevented further growth.

ETHEREAL AND ALCOHOLIC FLAX EXTRACTS

Flax powders have been extracted with ether and with alcohol by the use of the Soxhlet apparatus and also by suction of the cold reagent through the plant material in a Buechner funnel. The following summary of such experiments will indicate the methods and the results. In Experiment 126 # 4 flax powder was extracted with ether in a Soxhlet apparatus until practically no green color remained to be extracted. The powder was dried and made into a standard flax extract. Flask cultures, made as usual, were inoculated with # 7 *F. lini*. Abundant growth resulted. Some of the same powder was in a similar manner extracted with alcohol and the extracted flax made into flask cultures. The fungus grew well. As a check some of the same powder was made into a culture medium without having been extracted with ether or alcohol. No fungous growth took place. Evidently the ether and alcohol treatments had removed the toxic principle, at least below the inhibitive concentration. The ether and alcohol extracts were evaporated to dryness, taken up in a small amount of hot water, filtered, and made into culture media. When inoculated with the fungus a very slow development took place in the culture from the ether extractive, showing, however, only after 12 days of incubation. No growth of *Fusarium* occurred on the culture from the alcoholic extractives, although a contamination of *Monilia sitophila* took place and grew vigorously. Evidently

at least a portion of the toxic quality was transferred from the flax by means of the ether and the alcohol and hence is soluble in these reagents. In another experiment an alcoholic extract was made by treating the powder in a Buechner funnel with successive portions of alcohol, and applying suction. The extract was then evaporated to dryness, taken up in hot water, filtered and made into flask cultures. After inoculation with the fungus and incubation for eleven days with no growth resulting, a re-inoculation was made and no growth was developed. Another ether extraction experiment was tried in which the resulting extract was concentrated and then added to a series of tubes of Medium A. The first tube has 1/10 cc., the second 2/10 cc., etc., up to 5/10 cc. Apparently no growth took place in the more concentrated tube, a slight growth in the next lower, and so on down to the least concentrated tube in which a good growth took place, although not as rapid or abundant as in the check Medium A. Exact studies of the concentration limits for these extracts have not been made. In some few cases ether extractions have failed to produce toxic cultures, but lack of proper material has made it impossible to determine the cause of these failures, although it is suspected that it is associated with the question of the source of the flax powder. Attempts to obtain a crystallized product from these ether and alcohol extracts from rather small quantities of flax have so far failed, but will be renewed when there is a sufficient supply of dry flax of known toxicity available.

General Discussion and Conclusions

In experiments of the kind reported here there are two factors acting counter to one another. In the plant extract there are definite food values which are added to those included in the nutrients of the check medium. These would tend to increase the total growth of the fungus over the amount in the check cultures. The toxic quality must be sufficiently strong to overcome the nutritive value of the entire culture medium. In Fermi's solution used in the first studies (Reynolds, '26) the glycerine is a poor source of carbon for this fungus. Glucose, used in the check medium in the studies reported here, is a very satisfactory source of carbon. Thus while the dry weight of fungus in Fermi's

solution was usually less than 100 mgs., that in Medium A was usually from 200 to 300 mgs. The more dilute flax extracts used in the first study definitely retarded the growth of *Fusarium* in Fermi's medium, although no complete inhibition was found. In the more favorable Medium A the dilute flax extract served mainly to add nutrients and the toxic quality was thus masked. In the more concentrated flax media, from one-half to full strength, the toxic quality was evidently strong enough under some circumstances to over-balance completely the nutritive values and even kill the fungus. Since in many experiments the flax material was left long enough for the linase to hydrolyze at least a large part of the glucoside, linamarine, into HCN, acetone, and glucose, and the autoclaving produced sufficient heat to drive off the volatile toxic materials, it is clear that there must be in the flax a second toxic substance. In most of the experiments autoclaving of the flax extract did not so reduce its toxicity that the fungus could grow at the standard strength, yet occasionally at somewhat less than such a concentration the autoclaved medium did allow some growth. At about half-standard concentration autoclaving so reduced the toxicity that the added nutritive materials of the flax extract caused a distinctly larger fungous growth than in Medium A. At still lower concentrations autoclaving had little effect on the quantity of growth. It seems probable then that this second toxic material is somewhat thermostable although not completely so. Its other characteristics, as brought out in the experiments reported, are solubility in water, ether, and alcohol, and its essential non-volatility. It is somewhat specific for certain fungi and seems not to greatly influence others. While it does not dialyze readily it is not a coagulable protein. Its toxicity is rather low but when in sufficient amount it is absolutely deadly to this *Fusarium*.

Very little information appears in botanical writings concerning any such toxicity as reported here. Osterhout ('25) has reported that cells of *Valonia macrophysa* placed in sap extracted from similar cells quickly die. This result he attributed to the contrasting salt concentrations, but he did not eliminate the possibility that early death was due to other toxic factors. Prát ('27) heated extracts of several plant tissues and showed that living

cells from the same tissues die more quickly in these extracts than in isotonic sea-water of similar pH or in tap water. This seemed to indicate a special toxic action. O'Connor ('27) reported that specific, inhibiting, diffusible substances from plant and animal tissues, named by him "speciamines," inhibited growth of pollen tubes of "foreign pollens." Newton and his associates ('29) have noted an inhibiting action of wheat leaf filtrate on the germination of urediniospores and have suggested that phenolic substances are responsible for this action. It is probable that some of these observations, especially the last two mentioned, are in the same category as those reported for flax extracts.

Several materials known or supposed to exist in plants or in plant extracts should be considered in an attempt to determine the chemistry of the toxic material. Since formaldehyde may be formed from chlorophyll under certain circumstances (Warner, '14) and has been reported in the sap of green plants (Angelico and Catalano, '13), and since the flax extracts contain much leaf pigment it was thought that possibly toxicity might be ascribed to this compound. Tests were made for formaldehyde in these extracts but with entirely negative results. Mazzetti ('28) has shown that although boiled linseed oil develops bactericidal properties, these do not appear in the raw product from flax, almond, soybean, and castor bean. Since toxicity is found in unheated flax extracts, oil of the character of those named cannot be responsible for the inhibiting action. High relative acidity, coagulable proteins, and dialyzable substances have apparently been eliminated by experimental results. Toxic phenolic substances, such as suggested by Newton and his associates ('29), have not been specifically studied.

The different degrees of parasitism as shown by Broadfoot ('26) to exist in the different strains of *F. lini* should be considered in relation to resistance. In one experiment (# 101) # 2 *F. lini*, which in Medium A and dilute flax cultures produced less growth than # 7 *F. lini*, gave a much greater growth, especially in shoot extract which has been shown to be strongly toxic. It appears that the greater virulence of # 2 *F. lini* is associated with its ability to resist the toxic effects of flax, rather than with any special adjustment to nutritive qualities of its host.

That resistance to flax wilt and the toxicity of flax extracts may be associated phenomena is suggested not only by the more or less specificity of these extracts for *Fusarium lini*, but also by the relation of both phenomena toward changes of environment. It has been a rather common belief among those who have worked considerably with flax that it is easily influenced by the environment. Several specific evidences are discussed by Armstrong and Eyre ('12), and in the study of varietal distribution of HCN this apparent environmental effect was noted. The degree of toxicity of flax extracts seems also to vary with the environment surrounding the growing flax as evidenced by the markedly lower toxicity of the extracts from flax grown at St. Louis as contrasted with those from flax grown in New York. Resistance to flax wilt is known to vary with temperature as noted by Tisdale ('11) and studied by Jones and others ('26) more in detail, and it is possible that other environmental factors also are important.

It is realized by the writer that a number of important suggestions made here must be much more carefully studied, but the general trend of this investigation seems to be well established and details will be studied further as time will allow.

Summary

A general discussion of some of the essential problems in the physiology of plant disease is given, with emphasis upon the need of attacking them as a special project, with the active coöperation of variously trained specialists, rather than merely as an incident in routine pathologic investigations.

By cultural studies two kinds of toxic substances are recognized in flax extracts.

The glucoside, linamarine, producing HCN upon hydrolysis, has been discussed previously. Numerous analyses for HCN in flax extracts show a great variability of amount of this glucoside: its probable presence in larger amounts in the more resistant strains of flax; and its apparent close association with the young, actively functioning cells.

A new, somewhat thermostable, toxic material appears in the flax extracts of higher concentration. This material is apparently non-dialyzable, soluble in water, ether, and in alcohol; and varies

in quantity both in relation to environmental factors and in relation to variety of flax. In many extracts it is completely inhibitive to *Fusarium lini* at the normal concentration of the flax juice.

Bibliography

Armstrong, H. E., and Armstrong, E. F. ('10). The function of hormones in regulating metabolism. Ann. Bot. **25**: 507–519. 1910.

————, and Eyre, J. V. ('12). Studies on enzyme action. XVIII. Enzymes of the emulsin type. (III) Linase and other enzymes of Linaceae. Roy. Soc. London, Proc. **B85**: 370–378. 1912.

Angelico, F., and Catalano, G. ('13). Formaldehyde in the sap of green plants. Gaz. Chim. Ital. **43**: 38–43. 1913. [From Exp. Sta. Rec. **29**: 132. 1913.]

Angell, H. R., Walker, J. C., and Link, K. P. ('30). The relation of protocatechuic acid to disease resistance in the onion. Phytopath. **20**: 431–438. 1930.

Bishop, L. R. ('27). The estimation of cyanogenetic glucosides. Biochem. Jour. **21**: 1162–1167. 1927.

Broadfoot, W. C. ('26). Studies on parasitism of Fusarium lini Bolley. Phytopath. **16**: 951–978. 1926.

Dunstan, W. R., Henry, T. A., and Auld, S. J. M. ('06). Cyanogenesis in plants. IV. The occurrence of phaseolunatin in common flax. Roy. Soc. London, Proc. **B78**: 145–152. 1906.

————, ('07). Cyanogenesis in plants. VI. On phaseolunatin and the associated enzymes in flax, cassava, and the lima bean. *Ibid.* **79**: 315–322. 1907.

Eyre, J. V. ('12). The enzymes of Linaceae. Chem. News **106**: 167–168. 1912. [From Exp. Sta. Rec. **28**: 502–503. 1913.]

Hiers, G. S. ('26). A modified liquid sealed mechanical stirrer. Ind. and Eng. Chem. **18**: 1203. 1926.

Hursh, C. R. ('24). Morphological and physiological studies on the resistance of wheat to Puccinia graminis tritici Eriks. and Henn. Jour. Agr. Res. **27**: 381–413. 1924.

Jones, L. R. ('99). Certain potato diseases and their remedies. Vt. Agr. Exp. Sta., Bull. 72: 3–32. 1899.

————, ('05). Disease resistance of potatoes. U. S. Dept. Agr., Bur. Pl. Ind. Bull. 87. 1905.

————, ('26). Securing disease resistant plants: How important is it? Whose job is it? Science N. S. **63**: 342–345. 1926.

————, Johnson, J., and Dickson, J. G. ('26). Wisconsin studies upon the relation of soil temperature to plant disease. Wis. Agr. Exp. Sta., Res. Bull. 71: 25–31. 1926.

Jorissen, A. ('84). Recherches sur la germination des graines de lin et des amandes douces. Acad. Roy. de Belgique, Bull. III. **7**: 736–745. 1884.

————, et Hairs, E. ('91). La linamarine—nouveau glucoside fournissant de l'acide cyanhydrique par dédoublement et retiré du Linum usitatissimum. *Ibid.* **21**: 529–539. 1891.

Kunkel, L. O. ('26). Studies on Aster yellows. Am. Jour. Bot. **13**: 646–705. 1926.

Leonian, L. H. ('29). Studies on the variability and dissociations in the genus Fusarium. Phytopath. **19**: 753–868. 1929.

Link, K. P., Dickson, A. D., and Walker, J. C. ('29). Further observations on the occurrence of protocatechuic acid in pigmented onion scales and its relation to disease resistance in the onion. Jour. Biol. Chem. **84**: 719–725. 1929.

Massee, G. ('25). On the origin of parasitism in fungi. Roy. Soc. London, Phil. Trans. **B197**: 7–24. 1925.

Mazzetti, G. ('28). The bactericidal power of boiled linseed oil. Soc. Ital. Biol. Sper. Boll. **3**: 749–758. 1928. [From Chem. Abstr. **23**: 1150. 1929.]

McLean, F. T. ('21). A study of the structure of the stomata of two species of Citrus in relation to citrus canker. Torr. Bot. Club, Bull. **48**: 101–106. *1 fig.* 1921.

————, and Lee, H. A. ('21). The resistance to citrus canker of Citrus nobilis and a suggestion as to the production of resistant varieties in other citrus species. Phytopath. **11**: 109–114. *fig. 1.* 1921.

Monteith, J. ('24). Relative susceptibility of red clover to anthracnose and mildew. *Ibid.* **14**: 62–63. 1924.

Newton, R., and Anderson, J. A. ('29). Studies on the nature of rust resistance in wheat. IV. Phenolic compounds of the wheat plant. Canadian Jour. of Research **1**: 86–99. 1929.

————, Lehmann, J. V., and Clarke, A. E. ('29). *Ibid.* 5–35. 1929.

O'Connor, P. ('27). Inhibition of pollen growth by living tissue extracts. Roy. Dublin Soc., Sci. Proc. **18**: 477–484. 1927.

Osterhout, W. J. V. ('25). On the importance of maintaining certain differences between cell sap and external medium. Jour. Gen. Physiol. **7**: 561–564. 1925.

Pinckney, R. M. ('24). Effect of nitrate applications upon the hydrocyanic acid content of sorghum. Jour. Agr. Res. **27**: 717–723. 1924.

Prát, S. ('27). The toxicity of tissue juices for cells of the tissue. Am. Jour. Bot. **14**: 120–125. 1927.

Reynolds, E. S. ('24). Some relations of Fusarium lini and potassium cyanide. *Ibid.* **11**: 215–217. 1924.

————, ('26). Nutritional studies on Fusarium lini. Plant Physiol. **1**: 151–164. 1926.

Roe, J. H. ('23). The estimation of simple, soluble cyanogen compounds, making use of the principles of aeration. Am. Chem. Soc., Jour. **45**: 1878–1883. 1923.

————, ('24). The estimation of the hydrocyanic acid content of amygdalin by the aeration method. Jour. Biol. Chem. **58**: 667–669. 1924.

Rosenbaum, J., and Sando, C. E. ('20). Correlation between size of the fruit and the resistance of the tomato skin to puncture and its relation to infection with Macrosporium tomato Cooke. Am. Jour. Bot. **7**: 78–82. 1920.

Stakman, E. C., Parker, J. H., and Piemeisel, F. J. ('18). Can biologic forms of stem rust on wheat change readily enough to interfere with breeding for rust resistance? Jour. Agr. Res. **14**: 111–124. 1918.

Tisdale, W. H. ('11). Flaxwilt: A study of the nature and inheritance of wilt resistance. *Ibid.* **11**: 573–606. 1911.

Vavilov, N. I. ('14). Immunity to fungus diseases as a physiological test in genetics and systematics, exemplified in cereals. Jour. Genetics **4**: 49–65. 1914.

Walker, J. C., Link, K. P., and Angell, H. R. ('29). Chemical aspects of disease resistance in the onion. Nat. Acad. Sci., Proc. **15**: 845–850. 1929.

Warner, C. H. ('14). Formaldehyde as an oxidation product of chlorophyll extracts. Roy. Soc. London, Proc. **B87**: 378–385. 1914.

Weston, W. A. R. Dillon ('27). The incidence and intensity of Puccinia glumarum Eriks. and Henn., on wheat infected and non-infected with Tilletia tritici Winter, showing an apparent relationship between the susceptibility of wheat plants to yellow rust and to bunt. Ann. Appl. Biol. **14**: 105–112. 1927.

Willaman, J. J., and West, R. M. ('16). Effect of climatic factors on the hydrocyanic content of sorghum. Jour. Agr. Res. **6**: 261–272. 1916.

Young, P. A. ('26). Facultative parasitism and host ranges of fungi. Am. Jour. Bot. **13**: 502–520. 1926.

THE GENETIC ANALYSIS OF AN UNUSUAL RELATIONSHIP BETWEEN SELF-STERILITY AND SELF-FERTILITY IN NICOTIANA[1]

EDGAR ANDERSON

Geneticist to the Missouri Botanical Garden
Associate Professor in the Henry Shaw School of Botany of Washington University

AND

DOROTHEA DE WINTON

of the John Innes Horticultural Institution

A number of crosses between *Nicotiana alata*, *N. Sanderae*, and *N. Langsdorffii* were grown at the John Innes Horticultural Institution from 1923 to 1926 by the junior author. In most of these crosses the inheritance of self-sterility was quite straightforward, and the results obtained were substantially the same as those reported by East ('19), and East and Yarnell ('29). That is, the first generations consisted entirely of self-fertile plants, but on crossing the F_2 plants *inter se*, self-sterility reappeared in certain of the second-generation families. Among the plants of *N. alata* there was, however, a single plant (No. 15-2) whose cross-sterility relationships were exceptional and which gave rise to exceptional families when crossed with *N. Langsdorffii*. It is with the behaviour of No. 15-2 and its progeny that this paper is concerned. The results obtained from 1923 to 1926 with these plants are presented graphically in fig. 1, where they are contrasted with the results normally obtained upon crossing *N. alata* and *N. Langsdorffii*. Attention is called to the following peculiarities of the cross with No. 15-2: (1) The original exceptional plant was incompatible as a female with *N. Langsdorffii* though compatible as a male; (2) The F_1 was composed of self-sterile and self-fertile plants in approximately equal numbers—it will be remembered that normally in crosses between *N. alata* and *N. Langsdorffii* self-sterility would not appear until the second generation; (3) The self-sterile F_1's were compatible both as males and females with their self-sterile parent species *N. alata*, while with *N. Langsdorffii* they were compatible as males but incompatible as females.

[1] Much of the work reported in this paper was carried on under a National Research Fellowship in the Biological Sciences.

That is, they were *cross-sterile with their self-fertile parent and cross-fertile with their self-sterile parent.* No. 15-2 gave similar exceptional results when crossed with another self-fertile strain of tobacco, an ornamental garden variety of unknown ancestry obtained from Mr. E. A. Bowles. It bore small dark red flowers and was probably a self-fertile segregate from the cross *N. Langsdorffii* × *N. Forgetiana.*

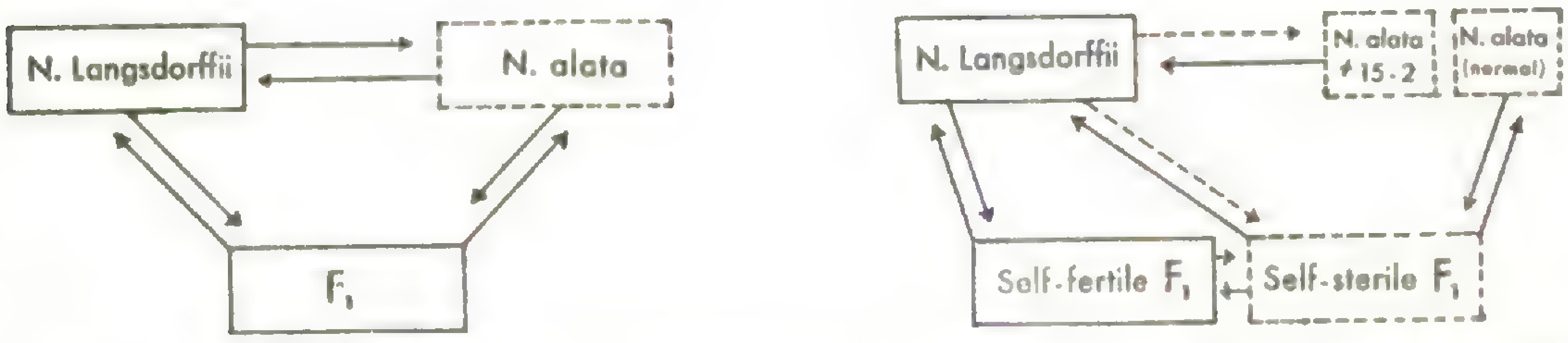


Fig. 1. Sterility and fertility relationships in normal crosses (left) and in hybrids with *N. alata* No. 15-2 (right). Solid lines indicate self- or cross-fertility; dotted lines, cross- or self-sterility.

All of these complications can be explained if we assume that No. 15-2 carried one self-sterility allelomorph of a slightly different nature from those normally present in *N. alata. Their* behavior is outlined by East and Yarnell ('29) as follows: "The action of these allelomorphs was such that a plant of constitution S_1S_2, when pollinated by pollen from a plant of constitution S_2S_3, produced two types of progeny, S_1S_3 and S_2S_3, due to the slow growth of the pollen tubes bearing the factor S_2." Continuing the notation developed by East and Mangelsdorf ('25) and East and Yarnell ('29), we may designate the exceptional allelomorph in No. 15-2 as S_F. This allelomorph operates like those designated by East and his students, but has the additional property of inhibiting the growth of pollen carrying the full fertility allelomorph S_f as well as that carrying S_F. Plant No. 15-2 was heterozygous for S_F and would set no seed with any pure self-fertile plant, since such pollen (all carrying S_f) would not grow fast enough to cause fertilization.

The other allelomorph of 15-2 was a normal self-sterility allelomorph. In the absence of precise tests with East's material we cannot tell just which one it was but may designate it S_n to indicate any one of the self-sterility allelomorphs. No. 15-2 is therefore represented in fig. 2 as of the genetic constitution S_FS_n.

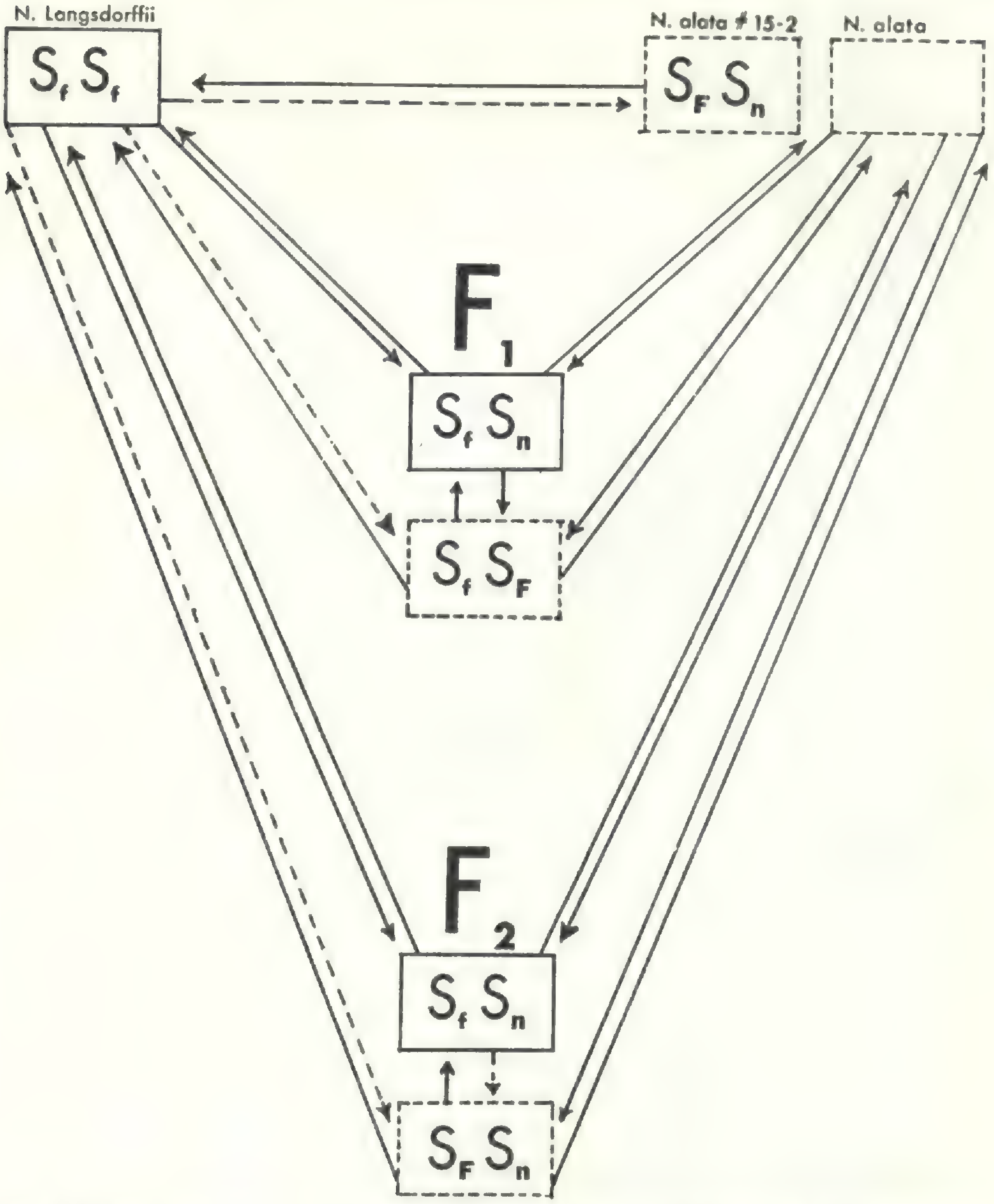


Fig. 2. Diagram showing the factorial analysis of the cross with *N. alata* No. 15-2. Solid lines indicate self- or cross-fertility; dotted lines, self- or cross-sterility.

When the pollen of 15-2 was applied to the stigmas of *N. Langsdorffii* (S_fS_f) both kinds of *alata* pollen (S_F and S_n) would affect fertilization, giving an F_1, half of which would be of the constitution S_fS_n, and half S_fS_F. The first would be self-fertile though carrying a self-sterility allelomorph (S_n). The second class would be self-sterile though carrying a self-fertility allelomorph (S_f). Furthermore, when pollinated with their self-fertile parent, *N.*

Langsdorffii, they would be cross-sterile, since the S_F gene would stop the S_f pollen precisely in the same way as it did in No. 15-2. On the other hand, when these self-steriles were pollinated with normal *N. alata* they would be cross-fertile. All these relationships are illustrated diagrammatically in fig. 2.

The above explanation therefore fitted all the known data and could be tested in several ways; four of these seemed worth trying. (1) A cross between a self-sterile F_1 and a self-fertile F_1 should give

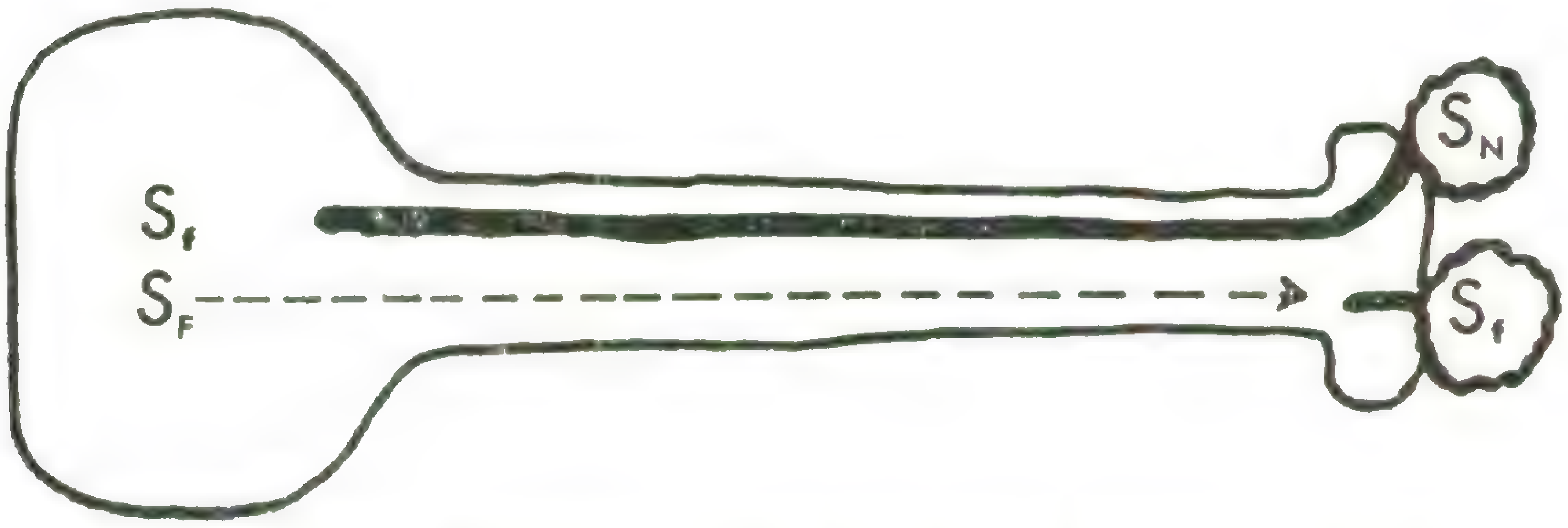


Fig. 3. Diagram of a self-sterile F_1 pistil pollinated with pollen from a self-fertile F_1. Dotted line shows antagonism between factors of the style and pollen. Cross fertile.

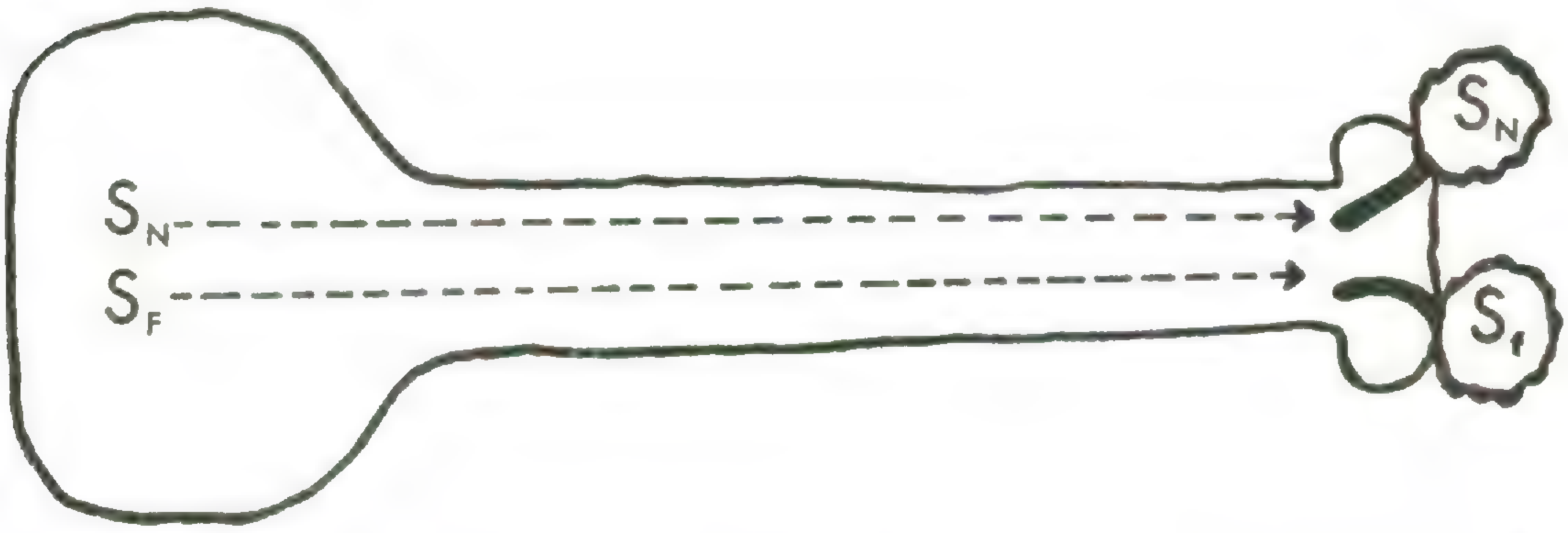


Fig. 4. Diagram of a self-sterile F_2 pistil pollinated with pollen from a self-fertile F_2. Dotted line shows antagonism between factors of the style and pollen. Cross sterile.

self-fertiles and self steriles in the F_2. (2) Though the self-sterile F_1's had been cross-fertile when pollinated by their self-fertile siblings the F_2 self-steriles should be cross-sterile when pollinated by their self-fertile siblings. These relations are diagrammed in figs. 3 and 4. Family 5N-30 (the result of pollinating self-sterile F_1, No. 29-12, by its self-fertile sibling No. 29-17) was grown to test these hypotheses. They were completely verified as shown in

TABLE I

POLLINATIONS ON SELF-FERTILE PLANTS

Plant No.	Fertile Matings			Sterile Matings		
	Self-pollinated	Pollinated by self-fertiles	Pollinated by self-steriles	Self-pollinated	Pollinated by self-fertiles	Pollinated by self-steriles
1	4					
2	4					
3	4					
4	4					
5	2					
7	4					
8	4					
9	3					
11	4					
12	3			1		
13	4					
18	4	4	2			
19	2			1		
20	2					
21	4					
22	2					
24	4					
25	3					
26	4					
27	4					
29	4					
30	4					
31	3					
32	4					
33	4					
35	4					
37	1					
38	4					1
40	2			2		
41	2					
42	4					
43	3					
44	3					
POLLINATIONS ON SELF-STERILE PLANTS						
6			1	4		
10				3		
14			1	5		2
15				7	16	13
16		2	1	8	5	2
17		2	3	4	5	11
23				3		
28		5	7	7		11
34				4		
36				3		
39	1			3		1
45				4		
46				4		
49				4		

table I. There were thirty-four self-fertiles and fifteen self-steriles. The self-steriles were furthermore not only cross-sterile when pollinated *inter se*, but were also cross-sterile when pollinated by their self-fertile siblings as is set out in the table.[1] (3) The self-sterile plants of the second generation, since they were carrying the factor S_F, should be sterile when pollinated by *N. Langsdorffii*. This prediction was also realized. Two unrelated strains of *Langsdorffii* were grown for the purpose. One, Family 1N-30, was from the same strain which had previously been used in the experiments. The other, Family K-30, consisted of six plants obtained from Kew Gardens. Both strains gave identical results. Both were fertile when pollinated with the F_2 self-steriles and both were cross-sterile when their pollen was used *on* the self-steriles. The data are summarized in table II. (4) The self-sterile F_2

TABLE II

RESULTS OF POLLINATING SELF-FERTILE AND SELF-STERILE F_2'S WITH N. LANGSDORFFII

	Fertile matings	Sterile matings
Self-fertile		
No. 2	4	0
No. 38	4	0
Self-sterile		
No. 14	0	1
No. 15	0	3
No. 16	0	4
No. 17	0	4
No. 28	0	6
No. 36	0	1

plants on the above hypothesis should (like the original *alata* grandparent No. 15-2) be heterozygous for S_F. Like it, therefore, when their pollen was used upon *N. Langsdorffii* they should yield progenies composed of self-sterile and self-fertile plants in approximately equal numbers ($S_fS_f \times S_FS_n \rightarrow S_FS_f + S_fS_n$). The appropriate pollinations were made at the John Innes Horticultural Institution, and several families were grown at the Missouri

[1] It must be remembered, of course, that Family 5N-30 was an F_2 from a very "wide" cross, and that, due to the recombination of modifying factors, cross- and self-incompatibility relationships could not be as clear cut as they would be in F_1, or in back-cross families. This whole matter is discussed below under the heading of "Modifying Factors."

Botanical Garden and at Washington University during the winter of 1930–1931. The results conformed completely with expectations and are briefly summarized in table III. With these results

TABLE III

RESULTS OF CROSSING N. LANGSDORFFII AND F_2 SELF-STERILES

Number of self-fertile plants	18
Number of self-sterile plants	8

the interpretation given on page 98 is thought to be well-established, and no further work is planned with this material. One additional test which *might* have been tried may be pointed out, since it indicates the complexities introduced by the factor S_F. A cross between a self-fertile F_2 and a self-sterile F_2 should give all self-steriles, in two intra-sterile, inter-fertile classes ($S_fS_n \times S_FS_n = S_fS_F$ and S_nS_F). A cross between these classes should produce both self-fertiles and self-steriles. In other words, on inbreeding, S_F produces a bewildering maze of interweaving classes in which self-sterility seems to be dominant to self-fertility, and self-fertility dominant to self-sterility, as the following examples show:

S. fert. S_fS_f	×	S. ster. S_FS_n	⟶	S. fert. S_fS_n	&	S. ster. S_fS_F
S. fert. S_fS_n	×	S. ster. S_FS_n	⟶	S. ster. S_fS_F	&	S. ster. S_nS_F
S. ster. S_fS_F	×	S. ster. S_nS_F	⟶	S. fert. S_fS_n	&	S. ster. S_FS_n

Modifying Factors

In so far as numbers and types of classes are concerned, the observed results are in strict accord with theoretical expectations. However, when we consider the ratios in which these different types appear, there is a wider departure from expectations. Nor is this at all surprising. Whether a plant shall be self-fertile or self-sterile is determined by the rate of pollen-tube growth in its style, and this is an exceedingly delicate reaction. Environmental

conditions affect it; East ('19) and Brieger ('27) have isolated genetic modifiers which change self-steriles into self-fertiles. If anything is at all surprising about the matter, it is the fact that, in a cross between parents differing in so many factors, and in dealing with a character so delicately adjusted as self-sterility, we should be able to find any genetic factors so clear-cut in their effect that their inheritance can be traced and their behavior in future generations confidently predicted.

As far as genetic modifiers are concerned, we should expect to get the greatest complexities in the second generation, for there recessive modifiers from either parent species would have a chance to recombine and turn otherwise self-sterile plants into self-fertiles, or vice versa. Next most difficult would be the back-crosses, while in the first generation we would expect the fewest complications. The results as reported below accord with these expectations. The only serious deviations from expectations are in the case of the second generation and in the back-cross to *N. Langsdorffii.*

In addition to the families grown in 1930 and 1931, there are the older records from 1924–26. These will all be considered together. In all the work pollinations were made in quadruplicate and when conflicting results were obtained the pollinations were repeated. The data will be discussed in the following order:

First generation—*N. Langsdorffii* × *N. alata*
Back-crosses to *N. alata*
N. alata × self-fertile F_1's
N. alata × self-sterile F_1's

Second generation
Self-fertile F_1 × self-fertile F_1
Self-fertile F_1 × self-sterile F_1
Self-sterile F_1 × self-fertile F_1
Back-crosses to *N. Langsdorffii*

FIRST GENERATION—N. LANGSDORFFII × N. ALATA

Data are at hand only for the original exceptional F_1, the result of pollinating *N. Langsdorffii* with the pollen of No. 15-2. We should expect self-fertiles (S_fS_n) and self-steriles (S_FS_f) in equal

numbers. The actual figures were twelve self-fertiles, sixteen self-steriles. The similar cross *Nicotiana* var. "Bowles" × *N. alata* 15-2 also yielded self-fertiles and self-steriles in approximately equal numbers.

BACK-CROSSES TO N. ALATA

N. alata × self-fertile F_1's.—Two families were grown in successive years, the results of pollinating two *N. alata* siblings by two different self-fertile F_1's. We should expect self-fertiles and self-steriles in equal numbers from such a mating. The actual results were as follows:

	$(S_xS_y) \times (S_fS_n)$	Number of self-fertile plants S_fS_x & S_fS_y	Number of self-sterile plants S_nS_y & S_nS_y
Family 8—1925	*N. alata* No. 35-1 × 29-7	26	17
Family 8—1926	*N. alata* No. 35-7 × 29-22	25	24

Cross- and self-fertility relationships could not be classified completely for Family 9-26, a cross between self-fertile F_1 No. 29-22 and *N. alata* No. 35-4, because it was segregating for an extreme form of male sterility in which no pollen was formed by some of the plants.

N. alata × self-sterile F_1's.—Four such families were grown. In each case we should expect self-fertiles and self-steriles in equal numbers. The results are as follows:

		Number of self-fertile plants	Number of self-sterile plants
Family 16—1925	29-6 × *N. alata* No. 35-2	19	22
Family 16—1926	29-8 × *N. alata* No. 35-2	24	20
Family 17—1925	*N. alata* No. 35-1 × 29-6	20	20
Family 17—1926	*N. alata* No. 35-1 × 29-8	19	17

SECOND GENERATION

Self-fertile F_1 × self-fertile F_1.—According to our interpretation, the genetic formula for the self-fertiles of the first generation was S_fS_n. On self-fertilization, or crossed with another self-fertile F_1, they should therefore have given all self-fertiles.

$$S_fS_n \times S_fS_n \longrightarrow S_fS_f + S_fS_n$$

This is on the hypothesis that the presence of the factor S_n in the tissues of the style will retard the growth of S_n pollen quite as effectively in a self-fertile plant as it would in a self-sterile plant. In case it did not do so a certain percentage of S_nS_n zygotes would result. As a matter of fact, two self-steriles did appear among some 200 seedlings, but in the absence of any precise data we can do no more than suggest that they may have arisen in this manner.

Self-fertile F_1 × self-sterile F_1 and *Self-sterile F_1 × self-fertile F_1*. —In each of these cases we should expect (in the absence of modifying factors) self-steriles and self-fertiles in equal numbers. In the first we should expect the following:

$$S_fS_n \times S_FS_f \longrightarrow \begin{array}{c} S_fS_F \\ \& \\ S_FS_n \end{array} + \begin{array}{c} S_fS_f \\ \& \\ S_fS_n \end{array}$$

In the reciprocal cross, S_F would inhibit the pollen tubes carrying S_f with the following result:

$$S_FS_f \times S_fS_n \longrightarrow S_FS_n + S_fS_n$$

Five families were grown. The first two are from a self-fertile F_1 × a self-sterile F_1, the last three from the reciprocal combination.

		Number of self-fertile plants	Number of self-sterile plants
14—1925	29-7 × 29-12	29	9
14—1926	29-7 × 29-12	18	2
15—1925	29-12 × 29-7	27	13
15—1926	29-8 × 29-7	17	3
5N—1930	29-12 × 29-17	33	14
		124	41
Expectations on the hypothesis outlined below		124	41

In each case there is a serious deficiency of self-steriles. Since the general situation seems to be the same in all five families, we may treat with the total of 124 self-fertiles and 41 self-steriles. If there had been no complications we should have obtained 82 of each. Two recessive modifiers, however, such as those already described by East ('19), would have so changed part of the 82 self-steriles that in the absence of precise pollination tests with

plants of known constitution they would have been classified among the self-fertiles. On this interpretation, if we let r and r_1 represent the two recessive modifiers, *N. Langsdorffii* would have been of the constitution $S_fS_frrr_1r_1$ and *N. alata* 15-2 of the constitution $S_FS_nRRR_1R_1$. The first generation self-fertiles would therefore have been of the constitution $S_fS_nRrR_1r_1$, and their self-sterile siblings of the constitution $S_FS_nRrR_1r_1$. The cross between self-steriles and self-fertiles would be diagrammed as follows:

Self-sterile F_1 × Self-fertile F_1	Self-fertile combinations	Self-sterile combinations
$S_FS_f\ Rr\ R_1r_1 \times S_fS_n\ Rr\ R_1r_1$	$S_fS_n\ RR\ R_1R_1$ — 1	$S_FS_f\ RR\ R_1R_1$ — 1
	$S_fS_n\ Rr\ R_1R_1$ — 2	$S_FS_f\ Rr\ R_1R_1$ — 2
	$S_fS_n\ RRR_1r_1$ — 2	$S_FS_f\ RR\ R_1r_1$ — 2
	$S_fS_n\ RrR_1r_1$ — 4	$S_FS_f\ Rr\ R_1r_1$ — 4
	$S_fS_nrrR_1R_1$ — 1	
	$S_fS_nrrR_1r_1$ — 2	Total self-steriles 9
	$S_fS_nRRr_1r_1$ — 1	
	$S_fS_nRrr_1r_1$ — 2	
	$S_fS_nrrr_1r_1$ — 1	
Modified self-steriles	$S_FS_frrR_1R_1$ — 1	
	$S_FS_frrR_1r_1$ — 2	
	$S_FS_fRRr_1r_1$ — 1	
	$S_FS_fRrr_1r_1$ — 2	
	$S_FS_frrr_1r_1$ — 1	
Total self-fertiles and pseudo self-fertiles..........	23	

We should therefore expect a ratio of 23 self-fertiles to 9 self-steriles. That is, out of every 32 plants we would expect one-half to be true self-fertiles. The other half would be divided into 9 self-steriles and 7 modified self-steriles which would be fertile with their own pollen, but cross-sterile in certain combinations. For 165 plants the expectations of a 23:9 ratio are (in whole numbers) 124 to 41, which is the exact number actually obtained.

BACK-CROSSES TO N. LANGSDORFFII

This hypothesis can be tested by examining the back-crosses. Clearly, such modifiers could not have come from *N. alata*, since the ratios obtained in back-crosses to that species were quite as regular as in the first generation. Therefore to test our hypothesis we turn to back-crosses between an F_1 self-sterile and *N. Langs-*

dorffii. In the absence of modifying factors we should again obtain a 1:1 ratio between self-fertiles and self-steriles.

$$S_fS_f \times S_FS_f \longrightarrow S_FS_f + S_fS_f$$

If two recessive modifiers are present, we would obtain a ratio of seven self-fertiles to one self-sterile. The data are available from one such family and can be summarized as follows:

	Number of self-fertile plants	Number of self-sterile plants
Family 18—1926 26-3 × *N. Langsdorffii* No. 29-8	30	3
Expectations on hypothesis outlined above	(29)	(4)

While the data are too meagre for final conclusions to be drawn the results from the one back-cross family are consistent with the results from the second generation families. Both point to *N. Langsdorffii* as having introduced recessive modifiers into the cross, which upon recombination in the second generation and in the back-cross to *N. Langsdorffii*, turned nominal self-sterile individuals into apparent self-fertiles. The ratios from both types of families are consistent with the hypothesis that two such recessive modifiers were introduced from *N. Langsdorffii.*

Linkage Between the Self-Sterility Allelomorphs and Other Genes

Family No. 5N-30 was a second generation from a cross between *N. Langsdorffii* and *N. alata.* These two species (or sub-species) differ by a large number of other characters beside self-sterility and self-fertility. Figure 5 and pl. 4 show typical flowers of each species. Some of the most outstanding differences are set out below in tabular form:

N. Langsdorffii	*N. alata*
Flowers green	Flowers white
Corolla-tube short	Corolla-tube long
Style proportionately short	Style proportionately long
Pollen blue	Pollen ivory

Fig. 5. Typical flower of *N. alata* (left) and of *N. Langsdorffii* (right) drawn to the same scale.

Nor are there any evident cytological complications which would hinder free recombination. Examination of the pollen mother cells with iron-aceto-carmine showed the reduction divisions to be regular. Certainly there was not more irregularity than existed in either of the parent species. Since the parent species differed in such a large number of characters it was thought probable that some of them would show linkage with the self-sterility allelomorphs. Such linkage has been reported for *Nicotiana* by Brieger and Mangelsdorf ('27) (anthocyanin flower color) and for *Antirrhinum* by Brieger ('30). Each plant of Family 5N-30 was accordingly scored for flower color, pollen color, tube length, and style length.

Corolla color.—As has been determined by a number of investigators the difference between the green-plastid corolla of *N. Langsdorffii* and the pure white-plastid corolla of *N. alata* is mainly due to a single factor, green being a simple dominant to white. The data

TABLE IV

NUMBER OF PLANTS OBTAINED IN A SECOND-GENERATION CROSS OF GREEN SELF-FERTILE AND WHITE SELF-STERILE

	Number of self-fertile plants	Number of self-sterile plants	Total
Green plastids	26 (25.3)*	10 (10.7)	36
White plastids	7 (7.7)	4 (3.3)	11
Total	33	14	47

* The figures outside the parentheses indicate the actual number of plants obtained. The figures within the parentheses show the number to be expected if self-sterility is inherited independently from plastid color.

from 5N-30 were in accord with this interpretation and also indicated that there is no appreciable linkage between the factor for plastid color and the self-sterility allelomorphs, S_1, S_2, S_f, etc. The data are given in table IV.

Corolla-tube length.—As is shown in fig. 5 and in pl. 4, this is the most conspicuous difference between the two parental species. It is due to at least four or five main pairs of factors and a number of minor modifying factors. Since there are only nine pairs of chromosomes in *N. alata* and *N. Langsdorffii,* the chances are good that at least one pair of factors affecting tube length might be linked with the self-sterility allelomorphs. From purely *a priori* assumptions we should therefore expect, upon crossing the long-tubed self-sterile species with the short-tubed self-fertile one, to find a higher percentage of self-steriles among the longest-tubed members of the second generation than among the shorter-tubed ones. The actual figures are as follows:

Tube length in millimeters	Number of self-fertile plants	Number of self-sterile plants	Per cent of self-sterile plants
30–39	12	3	20
40–49	16	6	27
50–59	5	5	50

Style length.—In *N. Langsdorffii* the style is shorter than the tube; in *N. alata* it is often much longer and the protruding stigmas are very conspicuous. While this is a highly variable character, even on a single plant, it can be roughly classified for purposes of comparison. The plants of 5N-30 were recorded as short-styled (like *N. Langsdorffii*) or long-styled (like *N. alata*) or intermediate. From the behavior of the character in later generations it is clearly affected by several pairs of factors. It is not surprising therefore that a higher percentage of the longer-styled plants were self-sterile, as the following table shows:

Proportional length of style	Number of self-fertile plants	Number of self-sterile plants	Per cent of self-sterile plants
Short	11	2	15
Intermediate	4	1	20
Long	18	11	38

Pollen color.—The pollen of *N. Langsdorffii* is a bright dark blue, that of *N. alata* is ivory or cream-colored, though the stamens themselves are often dark. The pollen of the F_1 plants was intermediate in color. In the second generation dark blue, ivory, and intermediates resembling the F_1 could be distinguished. The segregation is fairly clear-cut; probably not more than two or three pairs of factors are involved. One of them is evidently quite strongly linked with the sterility allelomorphs. It will be seen that we did not obtain a single self-sterile plant with dark blue pollen.

Pollen color	Number of self-fertile plants	Number of self-sterile plants	Per cent of self-sterile plants
Blue	7	0	0
Intermediate	19	7	27
Ivory	7	7	50

From the above discussion it is clear that in *Nicotiana* a number of genes are linked closely enough with the self-sterility allelomorphs to be detected readily. Linkage has been demonstrated and the linkage intensity calculated for the gene for anthocyanin flower color by Brieger and Mangelsdorf ('26). In the data reported above the linkage of one of the genes controlling pollen color and of at least one each of the genes for tube length and for proportional length of style is indicated. A careful study of other multiple factor differences between *N. Langsdorffii* and *N. alata* (as, for instance, leaf shape and stipule decurrence) would greatly extend the list.

For all of these genes Family 5N-30, a cross between two first-generation plants, was more like an ordinary back-cross than a normal second generation, due to the influence of the self-sterility allelomorphs. This fact is brought out diagrammatically in fig. 6, where the relationships of genes and the proportional contributions of the two parental species to the second generation are diagrammed, first, for an ordinary pair of Mendelian factors, and second, for the self-sterility allelomorphs S_F, S_f, etc. In the case of ordinary genes, if we consider the second generation as a whole, the two parental species have made equal contributions. In the case of the self-sterility allelomorphs all the male gametes carrying the S_f factors from *N. Langsdorffii* have been stopped.

As a result three-quarters of the self-sterility genes of the second generation, considered as a whole, have had their origin from *N. alata* and only one quarter from *N. Langsdorffii*. As far as the self-sterility allelomorphs are concerned the second generation Family 5N-30 was a back-cross to *N. alata*. To a lesser extent this was true as well for all the genes linked with the self-sterility allelomorphs.

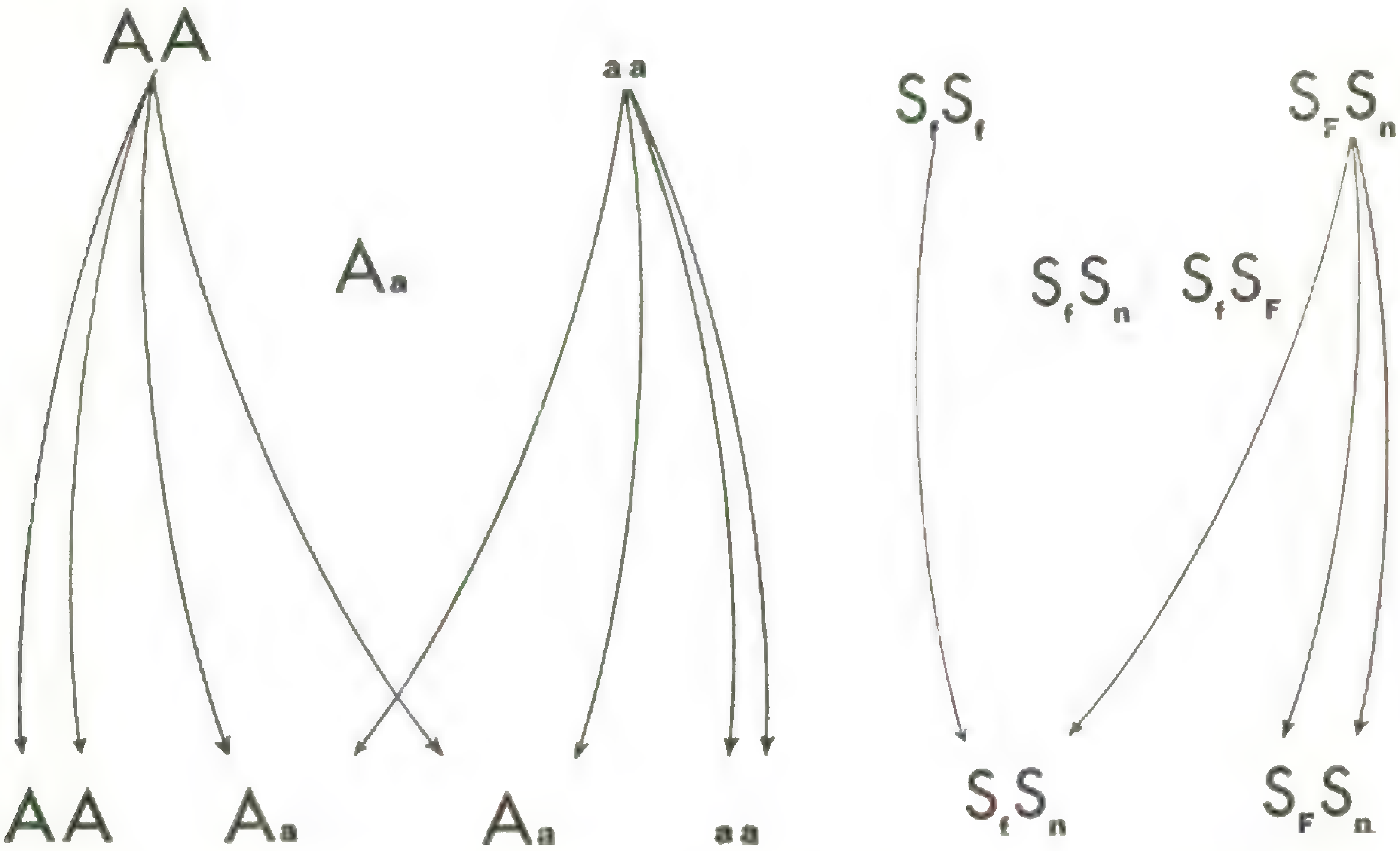


Fig. 6. Proportional contributions to the F_2: in the case of an ordinary pair of Mendelian factors (left); and in the case of the self-sterility allelomorphs (right).

The net result of such linkage should be quite striking in a species cross. The magnitude of the effect would depend upon the ratio between the non-crossed-over chromosome segment carrying the S factor and the chromatin as a whole. If we let n represent the average number of such segments then n-1 will represent that part of the chromatin not linked with the S factors. In the second generation this much of the chromatin will segregate normally and the relative contributions of the two species will be equal. If we let L stand for *Langsdorffii* chromatin and A for *alata* chromatin, the composition of the second generation can be represented as $2(n-1)L + 2(n-1)A$. For the segment containing the S factors, segregation will be abnormal. If the cross was made

as in the case of Family 5N-30, the composition of the second generation for this segment of chromatin will be 1L + 3A. Combining the two totals, the proportion of L and A chromatin in the second generation will be 2(n-1)L + 1L: 2(n-1)A + 3A which simplifies to (2n-1)L : (2n+1)A. In the absence of any genetical or cytological data as to the frequency of crossing-over in *Nicotiana* we can go no further with certainty. We know, however, that there are nine pairs of chromosomes. If, just as a guess, we take the average cross-over length as one-third of a chromosome, n will equal twenty-seven and the proportion of L and A chromatin in Family 5N-30 will be 53L : 55A.

That this is no mere idle speculation is proved by a comparison of East's ('16) tables and plates with those presented in this paper. In each case a second generation between *N. alata* and *N. Langsdorffii* was studied. In his case the selective effect of the S factors, if any, was in favor of *N. Langsdorffii*. In the cross reported here it was in favor of *N. alata*. And the tables and plates show that 5N-30 was definitely more like *N. alata* than the second generation families figured by him. Precise comparison is possible only for the length of corolla-tube. The data from both crosses are assembled graphically in fig. 7. Family 5N-30 is definitely more like *N. alata* than was East's F_2. The difference in the shape of the two curves is quite as striking as their position and is equally significant.

It may be remarked in closing that the complications introduced by self-sterility factors will be more striking in the case of species crosses than in crosses between closely related strains. In the latter case such anomalies as are due to linkage with the self-sterility allelomorphs will be apparent mainly in the ratios obtained between different types of offspring. In the case of species crosses, however, the chromatin in the neighborhood of the self-sterility allelomorphs will have accumulated a whole set of differing genes in the two species. In hybrids between them, reciprocal crosses may be characterized by gross morphological differences. This possibility has been alluded to by Brieger in his recent monograph ('30) and is, according to his brief reference, the explanation of the differences obtained in reciprocal crosses in *Antirrhinum* by Lotsy ('12) and Baur ('11).

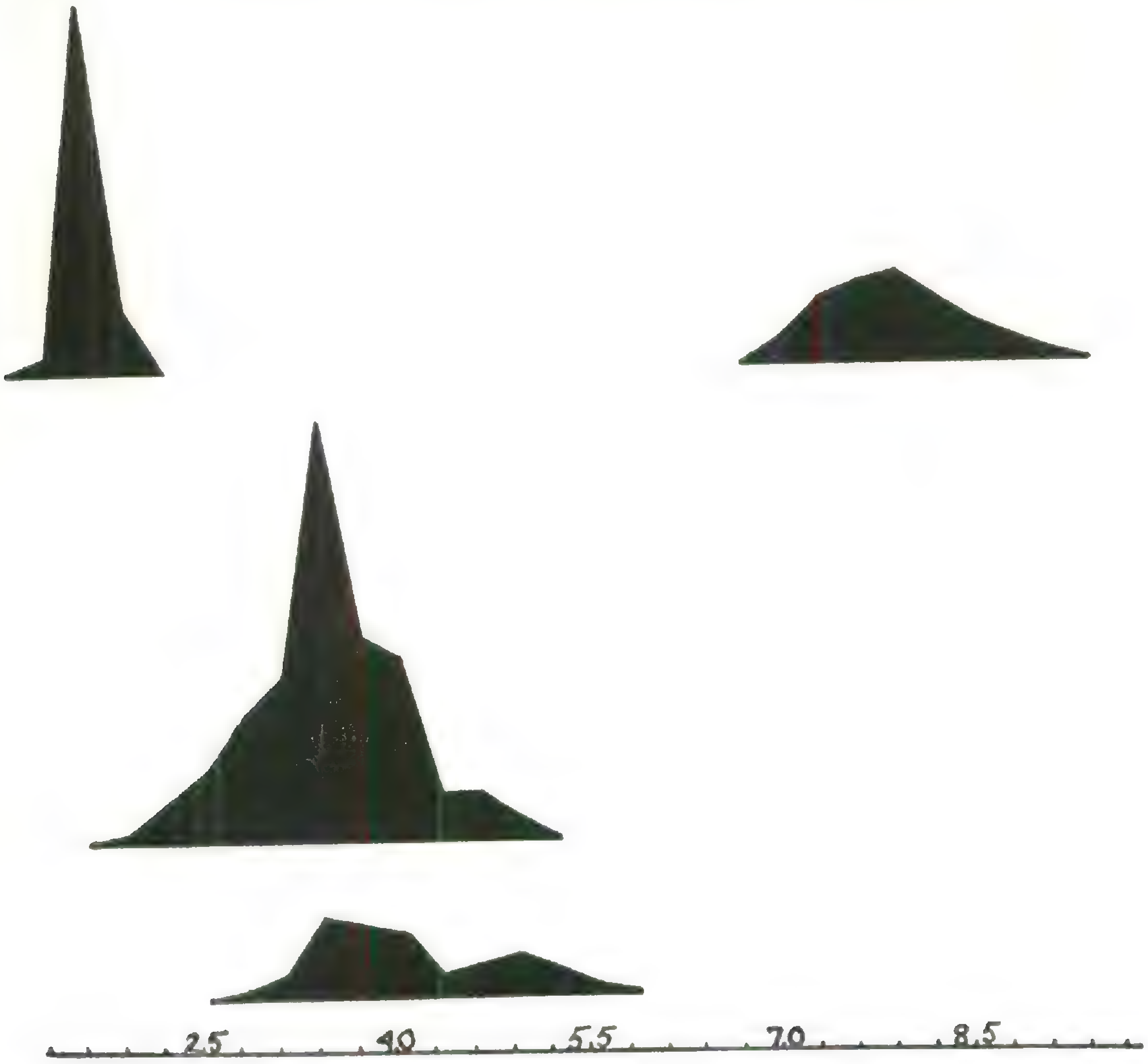


Fig. 7. Corolla length in centimeters for:

N. Langsdorffii	(upper left)	56 individuals	(data from East).
N. alata	(upper right)	49 individuals	(data from East).
East's F_2	(center)	163 individuals	(data from East).
Family 5N–30	(lower center)	47 individuals.	

(Each division of the scale represents 3 mm.)

Summary

I. In a number of crosses between self-fertile and self-sterile species of *Nicotiana*, a single plant of *Nicotiana alata* gave the following anomalous results:

1. It was female sterile when pollinated with self-fertile Nicotianas.
2. When used as a pollen parent with self-fertile Nicotianas half of the first generation hybrids were self-sterile.

3. These exceptional F_1 self-steriles were (as females) cross-sterile with their self-*fertile* parents!

II. These anomalies are interpreted as due to a single factor, S_F, belonging to the allelomorphic series S_f, S_1, S_2, S_3, S_4, etc., studied by East and his students. S_F has the same properties as the self-sterility allelomorphs previously described; that is, its presence in the cells of the style inhibits the growth of pollen tubes carrying the same factor. It differs from the factors hitherto described in that it also inhibits all pollen carrying the full fertility allelomorph S_f.

III. The F_1, F_2, and back-cross ratios of self-fertile to self-sterile are consistent with the assumption that two recessive modifying factors were introduced into the cross from *N. Langsdorffii*. When homozygous they turn otherwise self-sterile plants into apparently self-fertile plants (pseudo-self-fertiles).

IV. The S allelomorphs were found to be independent of the factor for green corolla color (plastid color). They are linked with one of the factors for pollen color and with at least one of the factors for length of corolla tube and for proportional length of style.

Attention is called to certain complications introduced into inter-species crosses by the interaction of the self-sterility allelomorphs. The morphological differences between the *Langsdorffii-alata* F_2 studied by East and the second generation family of the present experiment are interpreted on this basis.

Bibliography

Baur, E. ('11). Einführung in die experimentelle Vererbungslehre. Berlin, 1911.

Brieger, F. ('27). Über genetische Pseudofertilität bei der selbststerilen Nicotiana Sanderae hort. Biol. Zentralbl. **47**: 122–128. 1927.

————, ('30). Selbststerilität und Kreuzungssterilität. Gesamt. d. Physiol. d. Pflanzen. u. Tiere. Monogr. **21**: 395 pp. 1930.

————, and Mangelsdorf, A. J. ('26). Linkage between a flower color factor and self-sterility factors. Nat. Acad. Sci., Proc. **12**: 248–255. 1926.

East, E. M. ('16). Inheritance in crosses between Nicotiana Langsdorffii and Nicotiana alata. Genetics **1**: 311–333. 1916.

————, ('19). Studies on self-sterility. III. The relation between self-fertile and self-sterile plants. *Ibid.* **4**: 341–345. 1919.

————, and Mangelsdorf, A. J. ('25). A new interpretation of the hereditary behavior of self-sterile plants. Nat. Acad. Sci., Proc. **11**: 166–171. 1925.

East, E. M., and Yarnell, S. H. ('29). Studies on self-sterility. VIII. Self-sterility allelomorphs. Genetics **14**: 455–487. 1929.

Lotsy, J. P. ('12). Versuche über Artbastarde und Betrachtungen über die Möglichkeit einer Evolution trotz Artbeständigkeit. Zeitschr. f. indukt. Abst.- u. Vererbungslehre **8**: 325–333. 1912.

Explanation of Plate

PLATE 4

One flower each from the plants of Family 5N–30, a second generation from the cross *N. Langsdorffii* × *N. alata*. At the extreme left single flowers of the two parent species for comparison.

ANDERSON -SELF-STERILITY IN NICOTIANA

Annals
of the
Missouri Botanical Garden

Vol. 18 APRIL, 1931 No. 2

A MONOGRAPH OF THE GENUS SIDALCEA[1]

EVA M. FLING ROUSH

Formerly Jessie R. Barr Research Fellow in the Henry Shaw School of Botany of Washington University

Table of Contents

I

	Page
History of the genus	117
General morphology	120
Generic relationships	124
Specific variations, relationships, and general distribution	125
Hesperalcea	128
Malvastralcea	128
Eusidalcea	129
Perennes	129
Annuae	134
Abbreviations	136

II

Taxonomy	136
List of exsiccatae	218
Index to species	225

I

The History of the Genus

The genus *Sidalcea* was proposed by Dr. Asa Gray[2] in 'Plantae Fendlerianae' in 1849 with eight species, five of which were segregates from *Sida*. The name was compounded from *Sida*

[1] An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

[2] Gray in Mem. Am. Acad. N. S. **4:** 18. 1849 (Pl. Fendl. 18. 1849).

Issued June 30, 1931.

and *Althaea*, because of some fancied resemblance to the latter genus. The annuals constituted the typical section of the genus, and *S. diploscypha* must be interpreted as the type species.

During the next three decades very few new species were described and some of these were reduced to synonymy. Watson[3] in the 'Botany of California' recognized only five species indigenous to California. In 1885 Dr. Edward L. Greene[4] proposed six new Californian species and reinstated certain ones which had previously fallen to synonymy, thus making a total number of thirteen in his 'Synopsis.' In 1887 Gray[5] gave his "tentative distribution" of the perennials which he states "are hard to discriminate," adding that "those indicated by Prof. E. L. Greene may probably be maintained, as also one or two more." Greene,[6] in 'Flora Franciscana,' in 1891 added nothing of importance except the creation of the section *Hesperalcea* for the anomalous *S. malachroides*, which Gray[7] some time earlier had transferred from *Malva*.

E. G. Baker[8] in his 'Synopsis Malveae' accepted and listed all North American species known at that time, thus recording a total of eighteen, exclusive of three little-known South American species described by Turczaninoff[9] in 1863.

The latest and most comprehensive treatment of the genus is that given by Gray,[10] in the 'Synoptical Flora of North America' of 1897. Relationships within the group are indicated, based largely upon duration of growth, habit, time of flowering, inflorescence, stamineal phalanges, carpels, and pubescence. The earliest collections are cited and the geographical distribution as then known is given.

Since 1897 the number of species of *Sidalcea* has been more than doubled by the publication of descriptions of new species and varieties from western North America. Those of California

[3] Brew. & Wats. Bot. Calif. **1**: 83. 1876.
[4] Greene in Bull. Calif. Acad. Sci. **1**: 74. 1885.
[5] Gray in Proc. Am. Acad. **22**: 286. 1887.
[6] Greene, Fl. Francis. 102–106. 1891.
[7] Gray in Proc. Am. Acad. **7**: 332. 1868.
[8] E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 29. 1894).
[9] Turczaninoff, Bull. Soc. Nat. Mosc. **36**: 566. 1863.
[10] Gray, Syn. Fl. N. Am. 1^1: 302. 1897 (edited by B. L. Robinson).

have been given careful consideration by Jepson,[11] and those of the Rocky Mountain region have been treated by Rydberg.[12] However, these authors have included less than half of the number of described species.

In view of this situation and because of the vast amount of material that has accumulated in all the larger American herbaria from recent collections in western North America, and because of the great variation within the genus, it was thought advisable to study the genus *Sidalcea* in the light of all available material. The author has endeavored to explain the "perplexing variability" within the group by a close consideration of the possible ecological factors influencing variation, and to correlate this with the geographical distribution. An attempt has been made to clarify the hitherto involved synonymy, to formulate a workable key which shows the natural relationships, and to delimit the species sufficiently for easy recognition in the field and ready organization in herbaria.

Thanks are due those in charge of the herbaria of the following institutions for the loan of material in connection with this study: Gray Herbarium of Harvard University, United States National Museum, University of California, California Academy of Sciences, The Academy of Natural Sciences of Philadelphia, the University of California at Los Angeles, Pomona College, Rocky Mountain Herbarium (University of Wyoming), Leland Stanford, Jr. University, Oregon Agricultural College, University of Oregon, Herbarium of the University of Washington (deposited in the Washington State Museum), State College of Washington at Pullman, Willamette University, College of the Pacific, and A. O. Garrett Herbarium; also to those in charge of the herbaria visited: Field Museum of Natural History and Herbarium Greeneanum at Notre Dame University.

The author is indebted to Dr. George T. Moore, Director of the Missouri Botanical Garden, for the privileges of the herbarium and library of that institution. Sincere appreciation is expressed to Dr. Jesse More Greenman, Curator of the Missouri Botanical Garden Herbarium, for his helpful consideration and

[11] Jepson, Man. Fl. Pl. Calif. 628. 1925.

[12] Rydb. Fl. Rocky Mts. 558. 1917, and ed. 2. 558. 1922.

discussion of questions arising in connection with this monograph and for obtaining the loan of the abundant material examined; also to Dr. Mildred E. Mathias, Research Assistant, for invaluable aid in the preparation of the manuscript. Thanks are also due Dr. David H. Linder, Mycologist to the Missouri Botanical Garden, for the photomicrographs used in this publication, and to Dr. Roland V. LaGarde for the photographs of herbarium specimens.

General Morphology

The members of the genus *Sidalcea* are either annual or perennial herbaceous plants, often becoming ligneous at the base, or even suffruticose, as in the subgenera *Malvastralcea* and *Hesperalcea*.

Roots.—The annuals, comprising about one-sixth of the species, have a slight tap-root with small fibrous lateral roots. The perennials have either a creeping rootstock, or a strong woody root which assumes various shapes due to the physical conditions of the soil, some strikingly horizontal in shallow soil, others fusiform or otherwise thickened.

Stems.—The stems are erect or decumbent at the base, sometimes rooting along the lower part, or creeping and rooting at the nodes. They are simple or branched, few or several, and if several often caespitose or subscapiform. The annuals range from one to nine decimeters in height, whereas the perennials may reach two to three meters. Some are slender and wiry, others stout, fistulous or rarely succulent. The surface may be glabrous, glaucous, or with varying degrees of hirsute or stellate pubescence. The older parts are less pubescent than the younger.

Leaves.—There is such a striking difference in the cut of the leaves (pl. 8, fig. 1), coinciding with their position on the stem, that it is necessary to use the terms basal, middle cauline, and upper cauline in order to give an accurate idea of this variation. The basal leaves are rarely present on the mature plant, particularly in the annuals. As a rule, if present, they are orbicular, semi-orbicular, or cordate, lobed or palmately parted, varying in width from one to ten centimeters or more. The sinus may be closed, truncate, or open. The middle cauline leaves are often larger than the basal leaves, of the same general outline but

more deeply cleft, the lobes or segments varying in shape and in the degree of dentation. The upper cauline leaves are usually cleft almost to the base. The segments are narrow, entire or variously dentate. In appearance the surface may be green, glaucous, or cinereous. The leaves may be glabrous, pubescent, or puberulent, and the degree of pubescence differs on the two surfaces, usually greater (also more stellate) on the lower surface and on the veins. Young leaves are much more pubescent than older ones. The petioles may vary in length on a single individual from a few millimeters to at least five decimeters. There are no special markings on the petiole, and the pubescence is similar to that on the basal portion of the stem, or on the leaf-surface. There are two herbaceous or membranous, green or purplish stipules which are ovate, lanceolate-acuminate, linear, subulate, or filiform when parted, as in *Sidalcea diploscypha*, and may be glabrous, pubescent, or merely ciliate.

Pubescence.—In common with other Malvaceae the pubescence is predominately of the stellate type, and important in specific delimitation. There are, however, long simple or geminate hairs to which the term hirsute has been applied in this paper, but this condition is often intermixed with some form of radiate hairs. The branched hairs may be geminate, triradiate, or multiradiate, long or short, sparse, or if close forming a dense tomentum. If exceedingly short and minute, visible only under a lens, or harsh to the touch the term puberulent is used. At the base of the stems and on the petioles the hairs are often retrorse or deflexed, and on the leaves they are frequently appressed, particularly on the upper surface.

The form and degree of pubescence vary with the ecological and geographical conditions. Where there is abundant moisture from either the soil or atmosphere (fogs near the coast) or both, the prevailing type of pubescence is hirsute (*Sidalcea malvaeflora* and *S. neo-mexicana*), with or without an underlying layer of stellate hairs, especially in the inflorescence, or the plant may be glabrescent (*S. candida* and *S. Hendersoni*). In the more arid regions the prevailing pubescence is stellate, which may be dense, sparse, or so short as to be considered scurfy (some forms of *S. asprella*). In a transition region from much available moisture

to less moisture, or, as in the case of the annuals in the Sacramento Valley, where there is a short rainy season, then dryness, there is a mixture of the two prevailing forms of hairs. In a physiologically dry soil (subsaline) no pubescence develops except on the inflorescence, as in the typical *S. rhizomata* of Jepson. Those plants from alkali regions (types previously described as *S. nitrophila*, *S. confinis*, and *S. parviflora*) show a reduction of leaf surface, almost no hairs, and a whitening of the entire surface, with some indication of a thickening of the cuticle.

Inflorescence.—The inflorescence is terminal, few- to many-flowered, racemose, spicate, or subumbellate, rarely glomerate, either simple or paniculate, and rarely subscapiform. The rhachis, bracts, pedicels, and calyx usually have the same type of pubescence increasing in density toward the calyx, presenting characters of specific value. The bracts are ovate, deltoid, lanceolate, linear, subulate or setulose, and vary in length, rarely exceeding the pedicels after anthesis. They may be simple, bidentate or bifid (rarely trifid) to a greater or less degree, pubescent or merely ciliate, colorless, green, purplish, or purple-tipped. In a few cases they are membranous or even scarious. The pedicels are usually shorter than the calyx, although in some species they exceed it, especially in fruit (*S. neo-mexicana*). This character, therefore, is not of specific diagnostic value. The flowers are perfect or gynodioecious (pl. 5, figs. 1 and 2) (that is, with perfect and pistillate flowers on separate plants), and gynodimorphic (pl. 5, figs. 2 and 7) (that is, the pistillate flowers smaller than the perfect, with sterile or abortive stamens), and proterandrous, an adaptation for cross-pollination.

Calyx.—Bracteoles are present only in the subgenus *Malvastralcea*, although their presence has been reported in literature for the subgenus *Hesperalcea*. The calyx has a short tube, with a five-lobed limb, and may or may not be accrescent. The lobes are valvate, short-deltoid and almost obtuse, ovate and acute, or lanceolate and long-acuminate, variously pubescent without, arachnoid-villous within at the apex, ciliate, membranous, scarious, or herbaceous with one, three, or five prominent veins. In some species the lobes are purple-tipped (*S. Hendersoni*). The pubescence of the calyx is probably of more value in specific

differentiation than the length and shape of the lobes, and varies less within the species than the pubescence of other parts of the plant.

Corolla.—The prevailing color of the corolla is purple, varying from a deep dark purple to rose-purple (mallow purple), or even rose-pink. The only white-flowered species are probably *Sidalcea candida* and *S. malachroides,* although there are occasionally white-flowered forms in other species. In the type species, *S. diploscypha,* there is a very definite spot at the base of the petal which may vary from deepest purple to a colorless (greenish white) area, in which case it is spoken of as a "ghost" spot. The unguiculate petals are oblique, obcordate (if deeply notched), or merely truncate. On each side of the claw is a tuft of hairs which, meeting with those from the adjoining claw, forms the so-called "weel" (pl. 5, figs. 1 and 2). The apex may be entire, minutely denticulate, erose, retuse, emarginate, or deeply and broadly notched as in *S. malachroides.* The petals are not of special specific value because of the gynodimorphism in the plants.

Stamens.—The stamineal column is double (pl. 5, figs. 3 and 5), a character which delimits definitely this genus from all other malvaceous genera. The filaments are united into two series of phalanges, an outer and an inner. The outer series may separate from the column about the middle, at or near the summit. In the annuals there are five outer phalanges, arising near the middle of the column, which are broad, petaloid, convolute, antipetalous, and about five-antheriferous. This type of phalanx is best exemplified by the type species, *S. diploscypha* (pl. 5, fig. 4) and its nearest relative, *S. hirsuta.* In all, the inner series consists of ten linear, antisepalous, and diantheriferous phalanges. In the perennials (pl. 5, fig. 5) the outer phalanges are narrow, bi- or trifid, with the lobes diantheriferous, and arise near the summit of the column. The subgenus *Malvastralcea* has a stamineal column (pl. 5, fig. 6) which is not conspicuously double; the outer series of stamens being combined merely at the base into threes or fours. In the subgenus *Hesperalcea* (pl. 5, fig. 8) the stamens are few, small, apparently distinct, but usually the outer phalanges are bi- or trifid and occur at the summit of the

column. The anthers are reniform, one-celled by the confluence of their lobes at the apex, and dehisce transversely around the convex side, thereby becoming two-valved. The pollen is globose, spinescent, and extremely large, except in the subgenus *Hesperalcea*.

Pistil.—The pistil is composed of five to nine uni-ovulate carpels united about a central axis, with a corresponding number of styles united below. The free portions or branches of the styles are filiform and stigmatose the entire length of their inner face, and much exserted in the pistillate flowers.

Fruit.—The fruit (pl. 6) consists of five to nine membranous, reniform, apiculate carpels. This apiculation rarely persists in the mature fruit and may or may not be pubescent. The young carpel is apparently smooth (not wrinkled), and usually pubescent. As it matures the outer dorsal or dorso-lateral wall becomes variously favose, rugulose or reticulate, and if the transverse reticulations disappear the result is a sulcate or furrowed condition as in *Sidalcea calycosa.* The lateral wall has longer markings following very closely the nervation. The carpel is very rarely pubescent at maturity as in *S. hirsuta.* This smoothness or glabrosity of the immature carpel has been extensively used in previous descriptions of species; but, as the markings do not ordinarily appear until late in anthesis, this character becomes of little diagnostic value except in the case of mature fruit. The wrinkling may be augmented by drying. Throughout this study the antithetical terms "smooth and wrinkled," as well as "glabrous and pubescent," have been used to describe the carpellary condition. Although of value as a specific character in the genus, the carpel is of greater importance in indicating the natural grouping of species, as there is much individual variation in the form and degree of the markings. The seeds are of no diagnostic value.

Generic Relationships

The genus *Sidalcea* is placed in the tribe Malveae of the Malvaceae because of the definite and persistent central axis from which the carpels separate at maturity and because the stamineal column is antheriferous at the summit. It belongs in

the subtribe Eumalveae because of the filiform style-branches which are longitudinally stigmatose on the inner face.

Sidalcea is distinguished from *Sida* (to which certain species had formerly been referred on account of the lack of bracteoles) by the ascending cotyledons and descending radicle, as well as by the longitudinally stigmatose style-branches; from *Malva* and *Althaea* by the lack of bracteoles and fewer carpels; from *Malvastrum* by the style-branches and the habit; from *Sphaeralcea* by the uni-ovulate carpels; from *Callirhoë* by the soft, evanescent apiculation of the carpel; and from all the genera of the family by the separation of the stamens from the stamineal column in two series, an outer and an inner, with the filaments combined into definite sets or phalanges. The stamineal phalanges are best exemplified by the annual species, *Sidalcea diploscypha* and *S. hirsuta,* and are least evident in *S. malachroides* (pl. 5, figs. 4, 5, 6, and 8).

Specific Variations, Relationships, and General Distribution

The genus *Sidalcea* constitutes a group of plants inhabiting western North America from the Rocky Mountains in Colorado to the Pacific Coast, and from British Columbia south to the states of Lower California, Durango, Coahuila, and Nuevo Leon, in Mexico. The center of distribution for the genus is in the region of Eldorado County, California; more than half the species are indigenous to California and many are common to that state and one or more neighboring states (fig. 1).

As mesophytes, they are generally found growing along mountain streams, in moist meadows, along roadsides, about springs, in brackish or subalkaline marshes, and in the fog belt of coastal counties. If found in arid regions, they grow in moist but soon desiccated soil.

A discussion of the phylogeny of so variable a group is always more or less hypothetical, yet there are several criteria that may be used as probable evidence of certain tendencies, especially in connection with geographical distribution.

As to the probable origin of the group, it may be inferred that at the close of the Ice Age the genus migrated northward from

the Mexican plateau along two paths, the one following the

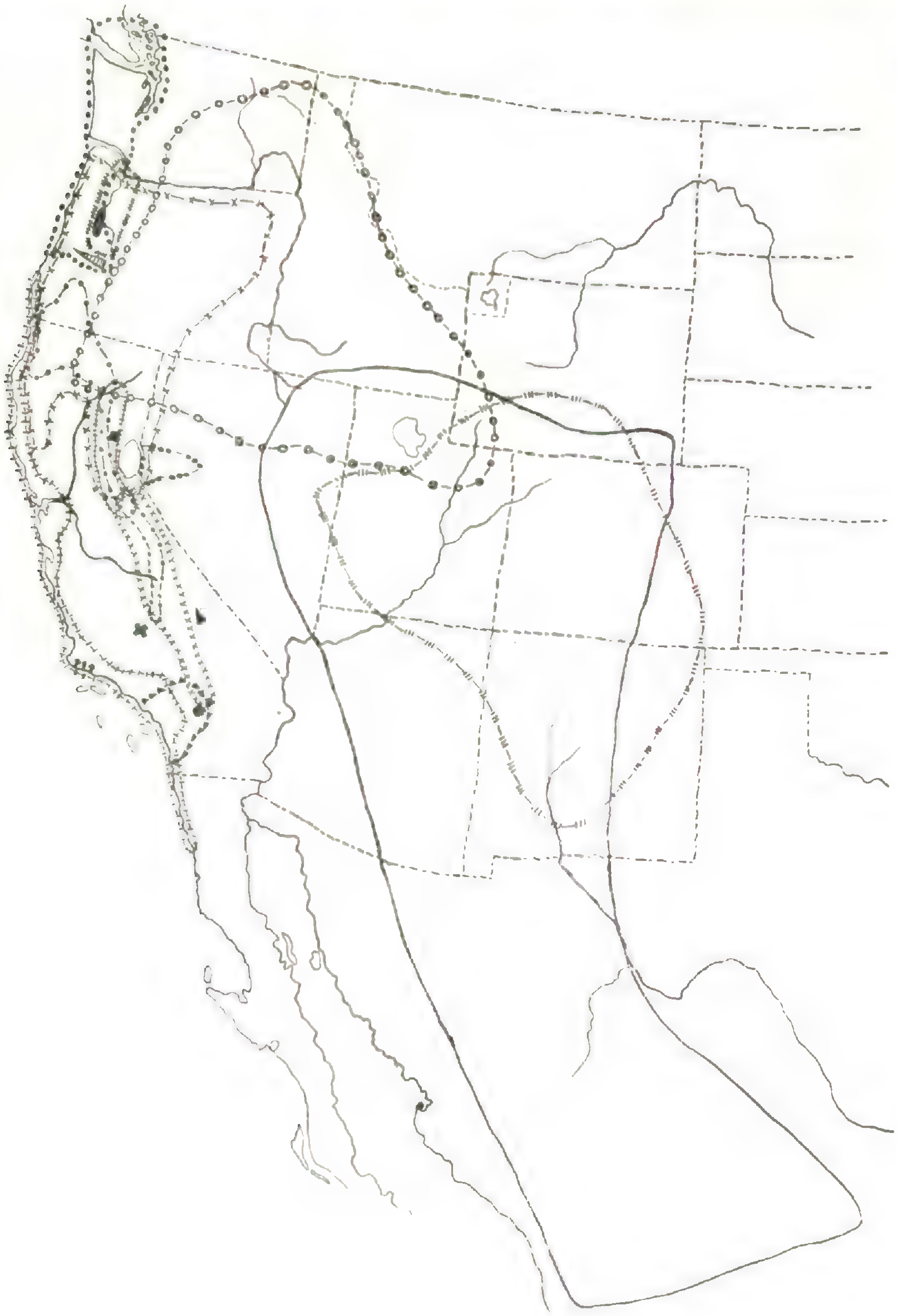


Fig. 1.

Rocky Mountains and the other traversing California. A discussion of these routes involves a consideration of the three

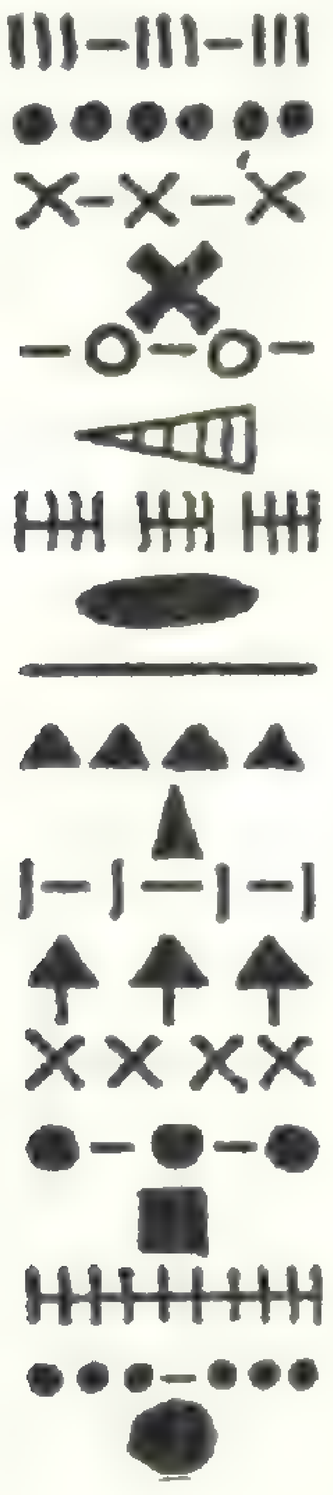
natural groups into which the genus readily falls, namely, the subgenera *Eusidalcea* (sections *Annuae* and *Perennes*), *Malvastralcea*, and *Hesperalcea*.

These groups doubtless had a common ancestor, which in some characters resembled the shrubby malvastrums of the subtropics, in others the more tree-like forms of genera not so closely related to the present *Sidalcea*. If certain characters common to the group as a whole be disregarded, then the characters used in this study as indicative of primitive and advanced conditions may be tabulated as follows:

PRIMITIVE	INTERMEDIATE	ADVANCED
Suffruticose	Herbaceous stem, ligneous at base	Herbaceous
Perennial	Perennial	Annual
Strong woody root	Root variously thickened	Slight tap-root
Much-branched stem	Branched or unbranched stem	Slightly branched stem
Branches leafy	Intermediate but chiefly floral	Branches chiefly floral
Slightly lobed leaves	Leaves variously lobed or cleft	Deeply palmately parted leaves

Figure 1.

Map of western North America showing general distribution of the subgenus *Eusidalcea*, section *Perennes*.



S. candida Gray
S. Hendersoni Wats.
S. spicata (Regel) Greene
S. spicata var. *ranunculacea* (Greene) Roush
S. oregana (Nutt.) Gray
S. oregana var. *Cusickii* (Piper) Roush
S. campestris Greene
S. virgata Howell
S. neo-mexicana Gray
S. neo-mexicana var. *parviflora* (Greene) Roush
S. neo-mexicana var. *Covillei* (Greene) Roush
S. malvaeflora (DC.) Gray
S. malvaeflora var. *californica* (Nutt.) Jepson
S. reptans Greene
S. asprella Greene
S. robusta Heller
S. glaucescens Greene
S. multifida Greene
S. pedata Gray

PRIMITITE	INTERMEDIATE	ADVANCED
Stamens apparently separate at summit of column	Outer stamineal phalanges evident, narrow, deeply cleft	Outer stamineal phalanges broad, petaloid, near middle of column
Small pollen	Intermediate	Large pollen
Smooth carpels	Carpels smooth to variously reticulate	Wrinkled carpels
Small carpels	Intermediate	Large carpels
Small embryo	Intermediate	Large embryo

Characters common to the subgenera as a whole and not considered in the tabulation are the prevailing gynodioecism and gynodimorphism, a generally accrescent calyx, and a spiciform or racemose inflorescence.

HESPERALCEA

The subgenus *Hesperalcea* with its one species, *S. malachroides*, may be considered the most primitive of the genus because it is a suffruticose, leafy branched perennial with a strong woody root and only slightly lobed leaves. The carpels are small and smooth, with a small embryo. The stamens are apparently separate at the summit of the column but in reality they are united into twos or threes in the outer series, and the pollen is very small. This is more nearly like the condition seen in *Adansonia* of the closely related Bombacaceae although habitally it most resembles *Malvastrum spicatum*. If this group be considered the most primitive, and, assuming that at one time it had a more or less continuous distribution along the California Coast, then, since it is now so rare along the northern California Coast, it may have remained on some higher point of land during subsequent submergence of the continental areas and later migrated to the more suitable moist habitat near the coast. From recent collections it seems to be proceeding northward from Mendocino County, California.

MALVASTRALCEA

The subgenus *Malvastralcea* simulates *Malvastrum* to such an extent that it was placed in that genus by Parish. It has all the primitive characters shown in *Hesperalcea*, except slight changes in carpels, stamens, and pollen. The carpels have very few wrinkles dorso-laterally, which do not always cross the dorsal

midnerve. The outer stamineal phalanges are more prominently cleft and merely united at the base into threes or fours. The pollen is larger. The species *Sidalcea Hickmani* was not found for many years outside of the Salinas Valley, California, then another collection was made at Tassajara Hot Springs not far distant, and much more recently a slightly modified form was collected in Marin County by Miss Alice Eastwood. *Sidalcea Hickmani* var. *Parishii* has been reported only from the west slopes of the San Bernardino Mountains, which indicates a most discontinuous distribution for this subgenus. Thus it may be surmised that this group had an almost parallel development with *Hesperalcea*, and is only a slightly more recent branch from the parent stock.

EUSIDALCEA

Perennes.—In the subgenus *Eusidalcea* the section *Perennes* shows the most divergent paths of migration, the one along the Rocky Mountains, the other through California. The two species *Sidalcea neo-mexicana* and *S. candida* occur along streams or in wet mountain meadows from Mexico to Wyoming and Idaho. Although of wider range than any others within the genus they are well defined with less variation individually and specifically than the California species. This may be due to the fact that the Rocky Mountains are older geologically than the California area, and thus it may be inferred that these two species have become more thoroughly established in their habitat. The great degree of variation exhibited in those *Perennes* that migrated through California may indicate that these species are a much more recent development and are still in a nascent state. The species of the section *Perennes* show all gradations of character between the other subgenera and the section *Annuae*, and are consequently difficult of specific delimitation. This variability is especially pronounced in those species covering a wide geographical range. Because of this puzzling variation and the conspicuous polymorphism and because the characters most affected are vegetative, it may be conceded that the response to so varied a topography and climatic conditions may account for the segregation of certain groups as rather large specific units with almost infinite local peculiarities, and the isolation of other much smaller

groups to very restricted areas. The *Perennes* constitute the intermediate group. The intermediate characters are: herbaceous perennials often becoming ligneous at the base of the stem, a variable root system, leaves variously lobed and parted even on the same individual, carpels which may be smooth, dorso-laterally reticulated (i. e., only on the angle), or entirely reticulate with short, close, fine meshes, and stamineal phalanges evident but very narrow, deeply bifid, and diantheriferous, and large pollen.

The path of migration of the *Perennes* in California was probably along the Sierra Nevada Mountains, and, not being boreal plants, they remained in the foothills and lower altitudes, very seldom above 5,000 feet. The greater number of species and individuals occur in those counties bordering Lake Tahoe on the west (particularly in Eldorado County). From the 3,000 herbarium sheets examined indications point to this area as being the probable center of distribution for the subgenus *Eusidalcea.*

It has not been possible to trace a direct lineal sequence through the *Perennes,* but certain species show relationships among themselves and to other groups that may be considered, and are illustrated on the accompanying hypothetical diagram (fig. 2). Specific segregation is, no doubt, due to a response to the environmental conditions of an extremely variable topography and climate, with consequent isolation along the route, or at the outermost limits of the area covered by the genus as a whole.

Sidalcea pedata, in all other characters similar to the perennials of *Eusidalcea,* has a stamineal column like that of the subgenus *Malvastralcea,* and may therefore be considered the connecting form between these two subgenera. This distinct species and *S. Hickmani* var. *Parishii* occur in neighboring regions. The scapiform habit and pedately parted leaves of *S. pedata* relate it to *S. multifida* of the foothills near Reno, Nevada, but the pubescence and inflorescence are totally different. It is not easy to separate the more erect forms of *S. glaucescens* in that region from *S. multifida,* but the restricted geographical range of the latter may be of assistance. *Sidalcea robusta,* while more closely related to *S. asprella* in its glaucous character and large showy

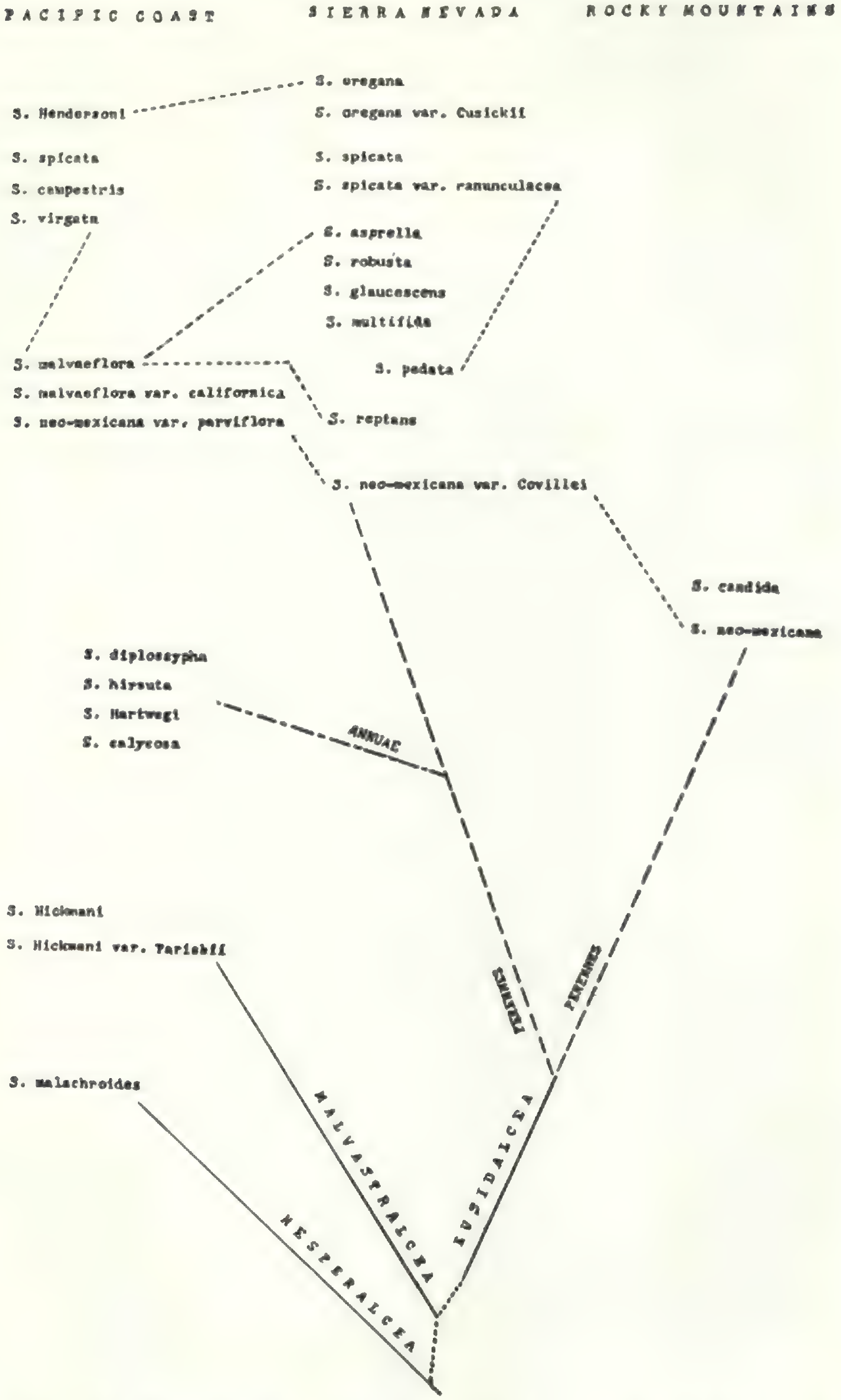


Figure 2. Chart showing probable relationships in connection with the general distribution within the genus *Sidalcea*.

Subgenera ————. Sections: Perennes — — — ; Annuae — - — -

Grouping of species indicates apparent relationships. The dotted lines indicate probable relationships between natural groups.

flowers and fruit, also bears some resemblance to *S. glaucescens*. This group might be called the *S. asprella-S. glaucescens* affinity.

Sidalcea asprella shows some relationship to the *S. malvaeflora-S. neo-mexicana* group by the cut of the leaves, pubescence, and size of carpel. *Sidalcea malvaeflora*, with the greatest longitudinal range along the coast and very polymorphic character, is most closely related, however, to *S. neo-mexicana*, the widest-ranging species of the inland regions, chiefly in the hirsute pubescence and calyx characters. A fairly direct though interrupted path of migration and relationship may be traced from the Nevada localities of *S. neo-mexicana* through its varieties *Covillei*, of Inyo County, California, and *parviflora*, of San Bernardino County, to the Los Angeles localities where the latter variety merges with the southern coastal forms of *S. malvaeflora*. More tendencies toward this relationship are shown by a comparison of those very dwarf forms (*S. confinis*, *S. parviflora* var. *Thurberi*) of *S. neo-mexicana* from the southern borders of New Mexico, growing in subalkaline soil, with the variety *parviflora* which also inhabits subalkaline areas or subalkaline marshes nearer the coast. In leaf form and pubescence *S. virgata* is not unlike the larger more decumbent forms of *S. malvaeflora*, but in inflorescence it is more like *S. campestris* of the Willamette Valley, Oregon. *Sidalcea reptans* has been placed by some authors under both *S. malvaeflora* and *S. spicata*. Although showing some resemblance to the former, very few characters of the latter are evident.

The idea of geographical strains, not separable specifically in the *S. spicata-S. oregana* alliance, may be considered here. If each of these species could be separated by definite geographical boundaries into lesser units, then more species or varieties could be delimited within the group. However, there is such an interweaving of these strains in the same localities, as well as over a rather extensive area, that tenable varieties can not be recognized. This group covers the regions of most varied topographical and climatic conditions, and therefore the resultant polymorphism is to be expected. Forms of *S. spicata* from Humboldt County, California, and Grant's Pass, Josephine County, Oregon, are so densely hirsute, have such large petals and robust habit (*S.*

eximia, type), and are so unlike some of the forms of the mountains of southeastern and middle Oregon as to be very confusing. If it be accepted that in the region covered by *S. spicata* there develops one strain with more hirsuteness and another strain with sparse or no hirsuteness but a more or less dense stellate-pubescence and that all gradations between these two strains may be found throughout the range and even on the same plant, rendering the recognition of varieties impracticable, the confusion resulting from attempts to segregate and name the great number of minutely different variants may be simplified. Certain characters, however, are relatively constant for this species: a more or less densely spicate inflorescence (small calyx, short pedicels) which may have a hirsute or stellate pubescence predominating, and long hirsute hairs on the lower part of the stem, or occasionally a more equal hirsute condition of the entire plant.

Sidalcea campestris, with a very restricted distribution in the Willamette Valley, Oregon, and generally resembling *S. spicata* in the hirsuteness of the stem and the inflorescence, has a much more lax inflorescence with long pedicels and lighter-colored flowers.

It is difficult to separate the northern California forms of *S. oregana* and the Sierra Nevada forms of *S. spicata* because of the stellate pubescence of both species in this region. *Sidalcea oregana*, however, has a harsh puberulence (glabrescent in the eastern forms), a different type of inflorescence, more elongate, less dense, with somewhat differently colored flowers, and a very different calyx which culminates in the peculiar campanulate calyx of its variety *Cusickii*. To the writer it is inconceivable that *S. campestris* is more closely related to *S. oregana* than to *S. spicata*. Those eastern Oregon forms which have a sparse hirsuteness mixed with the stellate pubescence may be due to some condition of the habitat rather than results of hybridization, although no experimental evidence has been brought forward to prove this assumption.

Sidalcea Hendersoni, the most northern species, may be related to *S. candida* through the lack of pubescence and smooth or smoothish carpels, and to the large forms of *S. oregana* in leaf character. In distance from the probable center of distribution

it might be considered a recent species; on the other hand, its more primitive characters and its relation to *S. candida* may indicate that it is an offshoot from the Rocky Mountain species, having gone far beyond them to a more northern and a moist habitat.

Annuae.—The section *Annuae*, with all the advanced characters above tabulated well developed, may be considered as a very recent offshoot from the section *Perennes*, and the plants have become adapted to the short season of rain and growth in the regions bordering the Sacramento and San Joaquin Valleys, California (fig. 3), and thus have developed the annual habit. Those plants nearer the coast are tending to become perennial by the development of roots along the base of the decumbent stem. The fact that they are gradually extending their range north, south, and west, may be only another evidence that the center of distribution for *Eusidalcea*, as given above, is in the region of Eldorado County, California. The *Annuae*, although closely related among themselves, are very distinct specifically in the carpellary characters but less so in vegetative ones, a condition just the reverse of that found in the more polymorphic and more widely distributed *Perennes*.

Sidalcea Hartwegi, which in all other respects is like the other annuals, has the outer stamineal phalanges of the perennials of *Eusidalcea* and is thus considered a transition form between the *Annuae* and *Perennes*.

The theory of hybridization has been advanced as a possible cause of the polymorphism and marked variability within this genus. However, the author at present has no direct evidence to advance in support of this theory. The variations exhibited seem to be the result of climatic, topographical, and geographical conditions. Shade and moisture seem to favor the development of thin leaves, fewer hairs or more simple hairs, and more luxuriant vegetative growth; exposure and little moisture or more arid conditions produce a tendency toward short, more-branched hairs (harsh puberulence in some), and more and deeply parted leaves; subalkaline or subsaline habitats result in reduced, thicker leaves with glaucous or glabrescent surfaces.

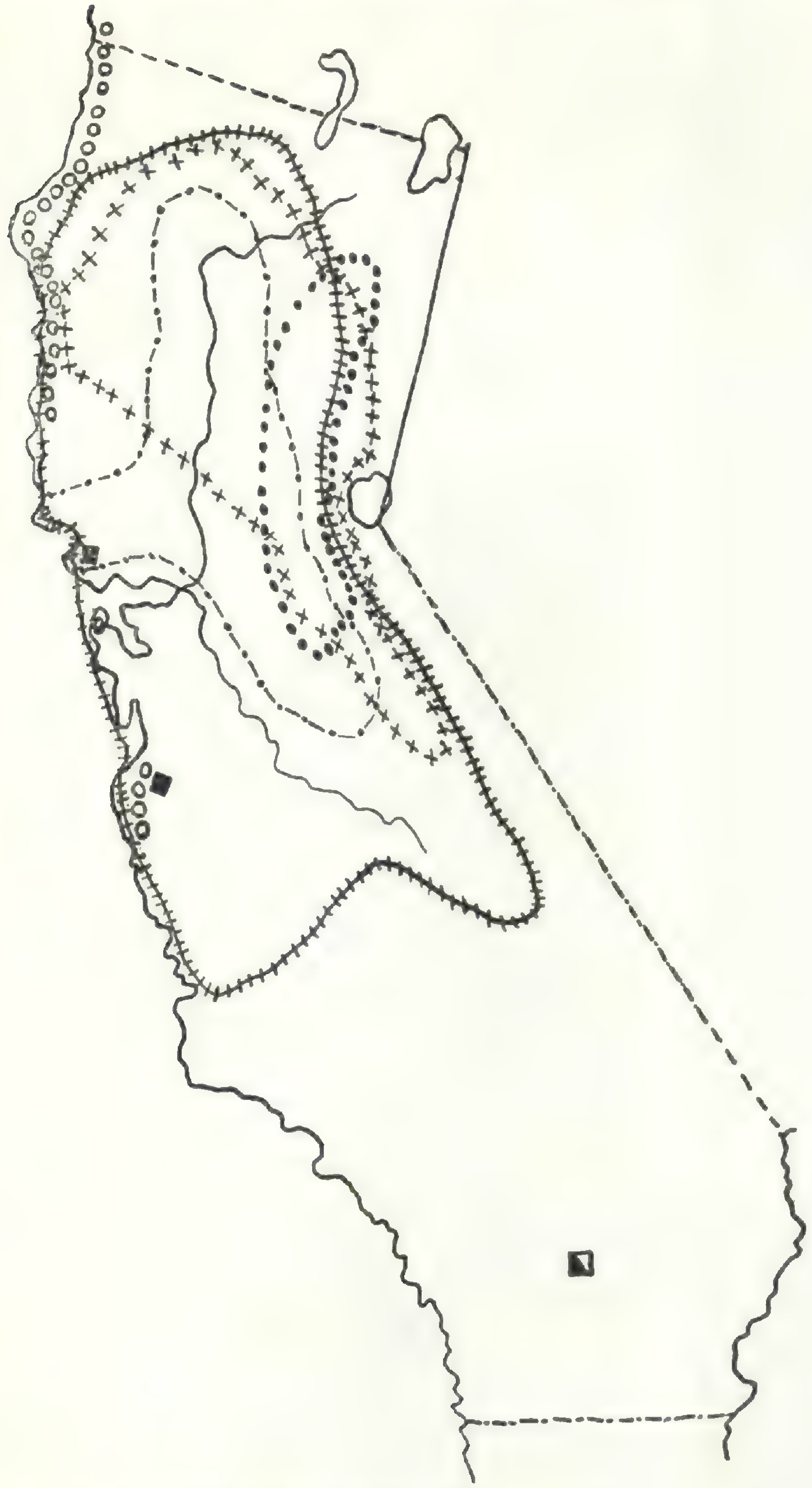


Fig. 3. Map of California, showing distribution of *Sidalcea*.

Subgenus *Eusidalcea*, section *Annuae:*

ǂǂǂǂǂ *S. diploscypha* (Torr. & Gray) Gray
●●●● *S. hirsuta* Gray
-●-● *S. calycosa* Jones
+++ *S. Hartwegi* Gray

Subgenus *Malvastralcea:*

■ *S. Hickmani* Greene
◪ *S. Hickmani* var. *Parishii* Rob.

Subgenus *Hesperalcea:*

○○○ *S. malachroides* (H. & A.) Gray

Abbreviations

Abbreviations indicating the herbaria where specimens cited in this monograph are deposited are as follows:

ANSP = The Academy of Natural Sciences of Philadelphia.
C = University of California.
CAS = California Academy of Sciences.
CP = College of the Pacific, Stockton, California.
F = Field Museum of Natural History.
Gar. = A. O. Garrett Herbarium, Salt Lake City, Utah.
G = Gray Herbarium of Harvard University.
M = Missouri Botanical Garden.
ND = Herbarium Greeneanum, University of Notre Dame.
O = University of Oregon.
OAC = Oregon Agricultural College.
P = Pomona College.
RM = Rocky Mountain Herbarium, University of Wyoming.
S = Leland Stanford, Jr. University.
SCW = State College of Washington, Pullman, Washington.
UCLA = University of California at Los Angeles.
US = United States National Museum.
W = Herbarium of the University of Washington, deposited in the Washington State Museum.
Wil. = Willamette University, Salem, Oregon.

II

Taxonomy

Sidalcea Gray in Mem. Am. Acad. N. S. **4**: 18. 1849 (Pl. Fendl. 18. 1849); Gen. Ill. **2**: 57. *pl. 120.* 1849; Walp. Ann. **2**: 150. 1851–52; Benth. & Hook. Gen. Pl. **1**: 201. 1862; Wats. Bot. King Exp. 46. 1871; Baill. Hist. Pl. **4**: 139. 1873; Brew. & Wats. Bot. Calif. **1**: 83. 1876; Greene in Bull. Calif. Acad. Sci. **1**: 74. 1885; Gray in Proc. Am. Acad. **21**: 409. 1886; *ibid.* **22**: 286. 1887; K. Schumann in Engl. & Prantl, Nat. Pflanzenfam. **3**^{6}: 41. 1890; Greene, Fl. Francis. 102. 1891; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 29. 1894); Greene, Man. Bay-Region Bot. 65. 1894; Gray, Syn. Fl. N. Am.

1[1]: 302. 1897; Jepson, Fl. West. Mid. Calif. 239. 1901, and ed. 2. 258. 1911; Abrams, Fl. Los Angeles & Vicinity, 247. 1904; Nelson in Coult. & Nels. Man. Bot. Cent. Rocky Mt. 317. 1909; Greene in Cyb. Columb. **1**: 33. 1914; Piper & Beattie, Fl. N. W. Coast, 238. 1915; Rydb. Fl. Rocky Mts. 558. 1917, and ed. 2. 558. 1922; Jepson, Man. Fl. Pl. Calif. 628. 1925.

Hesperalcea Greene in Pittonia **2**: 301. 1892; E. G. Baker, Synopsis Malveae Suppl. 109. 1894.

Erect annual herbs from a slight tap-root, or perennials from a strong woody root, frequently ligneous at base, rarely suffruticose, glabrous, stellate-pubescent, or merely stellate-puberulent. Leaves orbicular in general outline, variously lobed or parted; basal, middle cauline, and upper cauline leaves strikingly different (rarely of the same segmentation). Inflorescence terminal, racemose, spicate or subumbellate, singly or paniculately disposed; bracts ovate, lanceolate, linear, subulate or setulose; bracteoles none or rarely present. Flowers perfect or gynodioecious (with perfect and pistillate flowers on different plants) and gynodimorphic (the pistillate flowers smaller, deeper-colored and with sterile or abortive anthers). Calyx five-parted, often accrescent, the lobes deltoid, ovate or lanceolate, acute or acuminate. Petals dark purple, rose-pink, yellowish or white, obovate, entire or erose, emarginate or retuse, with a tuft of hairs at the base above each claw, forming the so-called "weel," the claw adnate to the stamineal column. Stamineal column sparsely stellate-hispid, of two series of phalanges (sets of united filaments), the outer antipetalous, arising near the middle or at the summit, either broad, petaloid, and convolute, 5-antheriferous, narrow, and bifid with diantheriferous lobes, or indistinct and stamens apparently separate; the inner series of 10 linear, antisepalous and usually diantheriferous phalanges. Anthers reniform, 1-celled on very short free filaments at the apex of each phalanx, usually yellowish, often purple or blue (rarely pink-tinged); pollen large, spinescent. Carpels 5–9 in a circle around a central receptacle; the filiform style branches as many as the carpels and longitudinally stigmatose on the inner face; ovule one in each carpel, peritropous-ascending, the micropyle inferior. Carpels separating at maturity from the receptacle, which is then marked by as

many obtuse, longitudinal processes as the number of carpels, subreniform, membranous, glabrous or pubescent, smooth or variously favose, reticulate or sulcate, beakless or with a short, soft, deciduous apiculation. Seed reniform; embryo arcuate-incurved, partially surrounding the soft endosperm, cotyledons foliaceous, cordate, conduplicate-infolded, radicle inferior.

Type species: *Sidalcea diploscypha* Gray in Mem. Am. Acad. N. S. **4:** 19. 1849 (Pl. Fendl. 19. 1849).

KEY TO THE SUBGENERA AND SECTIONS

Leaves orbicular in outline, variously lobed or parted (the upper cauline leaves cleft almost to the base); stamineal column conspicuously double, the outer phalanges broad and petaloid or narrow and bifid. .... *Subgenus I. Eusidalcea*

Annuals; outer phalanges broad and petaloid .... *Section 1. Annuae*

Perennials; outer phalanges narrow, deeply cleft .... *Section 2. Perennes*

Leaves flabelliform (or reniform-orbicular), scarcely or not at all lobed or parted; stamineal column not conspicuously double, the outer series of stamens combined merely at the base into threes or fours, approximating the inner at the summit; habitally like *Malvastrum* .... *Subgenus II. Malvastralcea*

Leaves vitiform; stamens few, the outer series apparently separate only at the very summit of the stamineal column .... *Subgenus III. Hesperalcea*

Subgenus I. Eusidalcea Jepson

Subgenus I. Eusidalcea Jepson, Fl. West. Mid. Calif. 239. 1901, and ed. 2. 258. 1911; Man. Fl. Pl. Calif. 628. 1925.

Annuals or herbaceous perennials, often ligneous at the base; leaves orbicular in outline, variously lobed or parted (the upper cauline leaves cleft almost to the base); bracteoles none; stamineal column conspicuously double, the outer phalanges broad and petaloid, about 5-antheriferous, or narrow and bifid, mostly 2-antheriferous. Sections 1 and 2.

Section 1. Annuae Roush

1. Annuae Roush, new section.

Annuals from a slight tap-root; mostly spring-flowering; leaves, except the basal ones, almost completely palmately (or pedately) parted; stamineal column conspicuously double, the five outer phalanges arising from near the middle of the column, petaloid-ampliate (except species no. 4), convolute in aestivation, mostly oblong and undivided, about 5-antheriferous on very short free

filaments at the truncate summit; the inner terminal phalanges mostly 10, linear and diantheriferous; mature carpels dorsally reticulate, rugulose, or favose with short meshes, or longitudinally striate-grooved; plants of California, the typical section. Sp. 1–4.

KEY TO THE SPECIES

a. Mature carpels dorsally rugose-reticulate, or favose with short meshes.
 b. Bracts palmately parted into filiform segments; plants tawny-hirsute; inflorescence laxly racemose to subumbellate...........*1. S. diploscypha*
 bb. Bracts entire or bifid, lobes narrowly linear.
  c. Plants more or less densely hirsute; inflorescence densely racemose, many-flowered...*2. S. hirsuta*
  cc. Plants glabrescent, or minutely stellate-puberulent; inflorescence racemose, few-flowered..............................*4. S. Hartwegi*
aa. Mature carpels dorsally striate-grooved longitudinally, about 7-ribbed ....*3. S. calycosa*

1. **S. diploscypha** (Torr. & Gray) Gray in Benth. Pl. Hartw. 300. 1848; in Mem. Am. Acad. N. S. **4**: 19. 1849 (Pl. Fendl. 19. 1849); Gen. Ill. **2**: 58. *pl. 120. f. 1–6.* 1849; Brew. & Wats. Bot. Calif. **1**: 84. 1876; Greene in Bull. Calif. Acad. Sci. **1**: 79. 1885; Gray in Proc. Am. Acad. **21**: 410. 1886; K. Schumann in Engl. & Prantl, Nat. Pflanzenfam. **3**^{6}: 41. 1890; Greene, Fl. Francis. 103. 1891; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 29. 1894); Greene, Man. Bay-Region Bot. 65. 1894; Gray, Syn. Fl. N. Am. **1**^{1}: 303. 1897; Jepson, Fl. West. Mid. Calif. 239 1901, and ed. 2. 259. 1911; Jepson, Man. Fl. Pl. Calif. 628. 1925. Pl. 5, fig. 4; pl. 7.

Sida diploscypha Torr. & Gray, Fl. N. Am. **1**: 234. 1838; and Suppl. 682. 1840; Hook. & Arn. Bot. Beech. Voy. 326. *pl. 76* 1840; Walp. Rep. **1**: 316. 1842.

Sidalcea diploscypha var. *minor* Gray in Mem. Am. Acad. N. S. **4**: 19. 1849 (Pl. Fendl. 19. 1849); Greene in Bull. Calif. Acad. Sci. **1**: 80. 1885; Gray in Proc. Am. Acad. **21**: 410. 1886; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 30. 1894); Gray, Syn. Fl. N. Am. **1**^{1}: 303. 1897; Jepson, Fl. West. Mid. Calif. 239. 1901, and ed. 2. 259. 1911.

S. secundiflora Greene, Fl. Francis. 103. 1891; Man. Bay-Region Bot. 65. 1894; Gray, Syn. Fl. N. Am. **1**^{1}: 303. 1897, in footnote; Jepson, Fl. West. Mid. Calif. 239. 1901.

Annual from a slight tap-root; stem erect, 1–7 dm. high,

slender and simple, or stouter and paniculately branched, pilose-hirsute throughout, intermixed with a short stellate pubescence; basal leaves orbicular-cordate, 1–2.5 cm. broad, merely crenate, early deciduous; cauline leaves 2–6 cm. in diameter, more or less deeply parted into 5–7 oblong, 2–3-lobed segments; stipules simple, linear-attenuate, or 2–5-parted into filiform segments; inflorescence few-flowered and laxly racemose, subumbellate, or cymose; rhachis, pedicels, bracts, and calyx densely stellate and pilose-hirsute; bracts conspicuous, up to 2.5 cm. long, palmately parted into 5–7 filiform segments; calyx-lobes lanceolate-subulate, as long as the bracts, the midvein prominent; petals varying in color from deep purple to rose-pink and with or without a conspicuous maculation at the base of the petal (sometimes developing a colorless area called a "ghost spot"); mature carpels depressed, subreniform, dorso-laterally rugulose with a more or less prominent dorsal midnerve.

Distribution: on grassy hillsides, in dry pastures and grain fields in northern middle California and along the coast from Humboldt County south to San Luis Obispo County.

Specimens examined:

California: shasta county—Oak Run, 21 May 1894, *Baker & Nutting* (C, ND); Oak Run, 21 May 1894, *Nutting* (C); tehama county—8 miles south of Vina, 29 April 1914, *A. A. Heller 11336* (ANSP, C, G); butte county—mesa east of Chico, April 1883, *Austin* (ND); Chico, April 1896, *Austin* (M); east of Chico, May 1896, *Austin 139* (ND, US); Chico, May 1897, *Bruce 1921* (P, S); fields, 8 May 1897, *Austin 1921* (G, US); near Clear Creek, 175 ft. alt., 1–15 May 1897, *H. E. Brown 215* (ANSP, C, F, M, S, US); near Chico, 5 May 1902, *Heller & Brown 5452* (ANSP, G, F, M, S, US); 12 miles north of Chico, 29 April 1914, *A. A. Heller 11336* (CAS, F, M, ND, OAC, S, US); yuba county—Marysville Buttes, 1893, *Blankinship* (C); plumas county—1877, *Austin* (F); calaveras county—near Milton, 18–30 May 1895, *Davy 1330* (C, G); mariposa county—summer of 1880, *Hollick* (US); inyo county—Round Valley, June 1925, *Mrs. G. E. Kelly* (CAS); colusa county—Mountain House, *K. Brandegee* (C); near College City, 1905, *King* (C, P); Indian Rancherio, Stony Ford, 1923, *Merriam* (CAS); yolo county—Capay Valley,

30 May 1893, *Blankinship* (C, G); near Madison, 29 April 1902, *Heller & Brown 5412* (ANSP, F, G, M, S, US); near Madison, 29 April 1902, *Heller & Brown 5414* (F, G, M, P, S, US); Rumsey, 7 May 1903, *C. F. Baker 2931* (C, G, M, ND, P, US); LAKE COUNTY—1884, *Curran* (G); Lakeport, June 1885, *K. Brandegee* (C); Lower Lake, May 1902, *Bowman 55* (S); near Lakeport, 1400 ft. alt., 12 May 1921, *Tracy 5539* (C); Kelseyville, 14 April 1923, *Blankinship* (CAS); near Lakeport, 19 May 1923, *M. S. Baker 2537* (S); NAPA COUNTY—Calistoga, 1888, *Parry* (M); 3–4 miles east of Angwin's, 1200 ft. alt., 21 May 1902, *Tracy 1576* (C); St. Helena, 1 April 1921, *Hunt* (CAS); Napa, 24 April 1924, *M. E. Jones* (P); SOLANO COUNTY—English Hills, 2–6 May 1891, *Jepson* (C); Vaca Mts., May 1892, *Jepson* (C); Montezuma Hills, 14 May 1892, *Jepson* (C, US); SACRAMENTO COUNTY—Elk Grove, May 1882, *Drew* (C); SAN JOAQUIN COUNTY—Stockton, 1890–91, *J. A. Sanford 349* (C); Hood's Peak, June 1893, *Michener & Bioletti* (C); CONTRA COSTA COUNTY—Pacheco Valley, May 1882, *Rattan* (S); 1884, *Curran* (S); Walnut Creek, May 1903, *Elmer 4316* (CAS, OAC, P, S); Concord, July 1903, *Elmer 4316* (M); ALAMEDA COUNTY—Newark, 6 May 1895, *Davy 1121* (C); SANTA CLARA COUNTY—4 miles south of San Jose, 1 May 1887, *Rattan* (S); between Saratoga Springs and the Village, 11 May 1888, *Leeds* (F); Mt. Hamilton, 9 June 1890, *Price* (C); Stanford University, 21 April 1895, *Rutter 123* (US); high hill, Stanford University, 16 May 1896, *Dudley* (S); between Smith Creek and Lick Observatory, 3000 ft. alt., 31 May 1907, *R. L. Pendleton 912* (C, P); 2 mi. from Gilroy, 6 May 1922, *Ferris* (S); Isabel Creek, Mt. Hamilton, 19 May 1923, *Ferris 4148* (P, S); near Coyote, 100 ft. alt., 17 May 1918, *Ferris 842* (S); HUMBOLDT COUNTY—1888, *Marshall* (C); near Elk Prairie, 11 June 1899, *Davy & Blasdale 5463* (C); Fort Seward, 400 ft. alt., 14 May 1914, *Tracy 4466* (C, US); MENDOCINO COUNTY—Ukiah, 6 May 1868, *Kellogg & Harford 111* (CAS, M, US); near Cahto, 18 June 1890, *K. Brandegee* (C); Snow Mountain, 22 June 1892, *K. Brandegee* (C); 30 June 1893, *Blankinship* (G); Potter Valley, 1600 ft. alt., April–May 1894, *Purpus 109* (*1090* or *1091*) (C); Potter Valley, April 1897, *Purpus 4056* (C); near Walkers Mt., 24 May 1899, *Blasdale 1022* (C); Sherwood Valley, 17 June 1899, *Dudley* (S);

near Yorkville, June 1901, *Carruth* (CAS); near Handley's, May 1903, *McMurphy 160* (S, US); Willits, June 1906, *Clark* (CAS); near Comptche, 23–29 June 1906, *H. A. Walker 312* (C); 1 mile north of Blue Rock, 28 July 1909, *McMurphy 836* (S); Ukiah, 13 June 1913, *Eastwood 3319* (CAS); near Ukiah, 30 April 1918, *Abrams 6981* (S); Willits, 21 May 1921, *Piper* (CAS); Potter Valley, 19 May 1925, *Eastwood 12713* (CAS); 15 miles n. of Ukiah, 18 June 1925, *Munz 9866* (P); along Eel River, near Hearst, 1600 ft. alt., 29 May 1927, *Bacigalupi 1558* (S); near Covelo, 5 June 1928, *Eastwood 15225* (CAS); SONOMA COUNTY—Petaluma, 10 April 1880, *Congdon* (S); 1892, *Bioletti* (C, F); Glen Ellen, 7 May 1898, *M. S. Baker* (C); between Santa Rosa and Sebastopol, 8 June 1905, *K. Brandegee* (C); Skaggs Springs, 3 June 1915, *Hawver* (CAS); *Samuels 29* (US); near Cloverdale, 20 April, *M. S. Baker* (S); MARIN COUNTY—Fairfax, May 1918, *Campbell* (CAS); San Rafael, 1 June 1920, *Jackson* (CAS); near Fairfax, 2 June 1929, *Sutliffe* (CAS); SAN MATEO COUNTY—woodside, Serpentine, Santa Cruz Peninsula, 17 April 1900, *Dutton* (S); west of Redwood City, 19 May 1906, *Dudley* (S, US); Serpentine back of Redwood City, 1 June 1920, *Abrams 7498* (S); SAN LUIS OBISPO COUNTY—near Morro, 22 May 1899, *J. H. Barber* (C); Morrow Bay, 10 May 1928, *Eastwood 15161* (CAS); near Cambrio, 18 May 1928, *Eastwood 15158* (CAS); WITHOUT LOCALITY—*Hartweg 1668* (G); 1846, *Fremont's Expedition 432* (G TYPE of *S. diploscypha* var. *minor* Gray, M, US); 1833, *Douglas* (G TYPE); 1853–54, *Bigelow* (ANSP, US); 1866, *Bolander 4813* (C, G, US); May 1884, Putah Canyon, *Jepson* (C); hilltops, 29 April 1900, *Atkinson* (S); Petrified Forest, 5 June 1915, *Eastwood 4586* (CAS); Dashielle, Mt. Sanhedrin, 22 May 1925, *Eastwood 12794* (CAS).

The difference in size of the types of *S. diploscypha* and its variety *minor*, in addition to the presence or absence of the maculation at the base of the petals, indicates why Dr. Gray so designated them. Examination of an abundance of more recently collected specimens proves definitely that in the absence of the dark purple spot a similar well-defined colorless area known as a "ghost" spot is developed (well shown in *Eastwood No. 12713*), so that in general in fresh material either the dark purple or the "ghost" spot is plainly visible. In specimens

collected by *K. Brandegee* between Santa Rosa and Sebastopol, 8 June 1905, there are all gradations from the darkest purple to the colorless area. The same is true for *Austin No. 139* and *Bruce No. 1921*. The matter of size as a varietal distinction does not hold, as is shown by the fact that the specimens cited, as well as many others which have the maculation, are much larger than Gray's type of the species.

Specimens which may be considered authentic for Greene's *S. secundiflora* are very slender unbranched forms with few flowers which are more laxly racemose than some of the more robust branching forms. The inflorescence can scarcely be called "secund" in any of these plants, as all gradations from the laxly racemose to the cymose or even the subumbellate condition are present throughout the group. Variation in the degree of hirsuteness in the species has led to the confusion of those less hirsute with *S. Hartwegi*, but the presence of the palmately parted "spider-like" filiform bracts, as well as the less rugose carpels, makes *S. diploscypha* definitely distinct.

This is a strikingly beautiful species which, as a cultivated plant, even though an annual, should rival some species of *Lavatera* and *Malva*.

2. **S. hirsuta** Gray in Smiths. Contr. **3**: 16. 1852 (Pl. Wright. **1**: 16. 1852); Torr. in Pacif. R. R. Rept. **4**: 72. 1857; Walp. Ann. **4**: 309. 1857; Gray in Proc. Am. Acad. **21**: 410. 1886; Greene, Fl. Francis. 103. 1891; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 29. 1894); Greene, Man. Bay-Region Bot. 65. 1894; Gray, Syn. Fl. N. Am. **1**^{1}: 303. 1897; Jepson, Man. Fl. Pl. Calif. 629. 1925. Pl. 6, fig. 1.

S. delphinifolia Gray in Benth. Pl. Hartw. 300. 1848, not *Sida delphinifolia* Nutt.; in Mem. Am. Acad. N. S. **4**: 19. 1849 (Pl. Fendl. 19. 1849); Gen. Ill. **2**: 58, *pl. 120, f. 10–12.* 1849; Walp. Ann. **2**: 151. 1851–52, as to name only.

S. Hartwegi Brew. & Wats. Bot. Calif. **1**: 84. 1876, as to description and synonymy; Greene in Bull. Calif. Acad. Sci. **1**: 78. 1885.

Annual from a tap-root with strong lateral roots; stem erect, stout, 1-8 dm. high, strict or with erect branches, usually glabrous

below, soft-hirsute above; basal leaves round-cordate, small, crenately lobed, early deciduous; cauline leaves 3–8 cm. broad, almost completely palmately parted into 7–9 narrowly linear and entire acute segments, the younger hirsute on the lower surface and the petiole, the older glabrous except on the veins beneath; stipules purplish, lanceolate-attenuate or subulate, 3–12 mm. long, ciliate; inflorescence up to 20 cm. long, densely spicate, leafy at base, rhachis and pedicels tawny-hirsute; bracts often purplish, linear, bifid; calyx densely tawny-hirsute intermixed with a close stellate tomentum, deeply lobed, the lobes triangular-lanceolate, long-acuminate, ciliate; petals rose-purple, emarginate and erose, 15–25 mm. long; mature carpels large, favose-reticulate or deeply favose-areolate, more or less stellate-pubescent.

Distribution: in low and wet but soon desiccated ground in the valleys of the Sacramento and Stanislaus Rivers from Butte County to Merced County, California.

Specimens examined:

CALIFORNIA: BUTTE COUNTY—Chico, wheat fields, 27 April 1885, *Gray* (G); Rancho Chico, May 1878, *Bidwell* (G); Chico, 1887, *Parry* (M); plains east of Chico, April 1896, *Bruce 193* (US); plains east of Chico, July 1896, *Bruce 693* (M); plains along sloughs, April 1897, *Bruce 1924* (P); fields near Chico, May 1897, *Austin 1924* (US); near Biggs, 15 May 1902, *Heller & Brown 5557* (ANSP, F, C, P, M, S, US); Table Mountain, Olive Ranch north of Oroville, 23 May 1912, *A. A. Heller 10751* in part (S, US); Chico-Centerville road, 3 miles from Chico, 16 May 1915, *A. A. Heller 11871* (ANSP, CAS, F, G, M, OAC, S, US); along highway, 9 miles north of Chico, 8 May 1926, *A. A. Heller 13937* (US); 10 miles north of Chico, 3 May 1927, *A. A. Heller 14362* (ANSP): ELDORADO COUNTY—1866, *Rattan* (S); CALAVERAS COUNTY—road near Jenny Lind, 500 ft. alt., 12 May 1928, *Stanford 971* (CP); between Valley Springs and Wallace, 1 May 1923, *Steinbeck* (CAS); STANISLAUS COUNTY—Knights Ferry, 7 May 1853–4, *Bigelow* (G, US); MERCED COUNTY—Merced, 23 April 1915, *Eastwood 4392* (CAS, US); WITHOUT LOCALITY—1868–9, *Kellogg & Harford 110* in part (G); *Hartweg 1667* (G TYPE); 1838–42, McCombs Exp., *Newberry* (US).

Dr. Gray[13] in the original treatment of the genus *Sidalcea* described the Hartweg collection (*No. 1667*) as *Sidalcea delphinifolia* and erroneously interpreted this species as being conspecific with the *Sida delphinifolia* Nutt. which is *Sidalcea malvaeflora.* He later recognized this case of mistaken identity and renamed the *Sidalcea delphinifolia,* designating it as *S. hirsuta.* Dr. Greene later took up the name of *S. delphinifolia,* applying it to the true *S. malvaeflora* of the coastal region which is the same as the *Sida delphinifolia* of Nuttall.

The species is worthy of cultivation because of the long raceme of very large rose-purple flowers, as contrasted with the tawny hirsuteness of the vegetative parts and the calyx.

3. **S. calycosa** Jones in Am. Nat. **17**: 875. 1883 (here published as *Sidalcia*); Gray in Proc. Am. Acad. **21**: 410. 1886; *ibid.* **22**: 286. 1887; Greene, Fl. Francis. 104. 1891; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 29. 1894); Greene, Man. Bay-Region Bot. 65. 1894; Gray, Syn. Fl. N. Am. **1**[1]: 303. 1897; Jepson, Fl. West. Mid. Calif. 240. 1901, and ed. 2. 259. 1911; Man. Fl. Pl. Calif. 629. 1925.

Pl. 6, figs. 3 and 4.

S. sulcata Curran acc. to Greene in Bull. Calif. Acad. Sci. **1**: 79. 1885; Gray, Syn. Fl. N. Am. **1**[1]: 303. 1897; Jepson, Fl. West. Mid. Calif. 240. 1901, and ed. 2. 259. 1911.

S. rhizomata Jepson, Man. Fl. Pl. Calif. 629. 1925.

Annual (tending to become perennial by the rhizomatously rooting base); stems simple or much branched, slender or more or less succulent, green or purplish, erect or ascending, up to 7.5 dm. high, the decumbent base often rooting freely, glabrous or sparingly hirsute, especially above; basal leaves orbicular, up to 10 cm. wide, crenate or slightly lobed, petioles up to 3 dm. long; cauline leaves almost completely parted to the base into 5–11 oblanceolate or cuneate segments, the segments entire or dentate at the apex, somewhat hirsute and ciliate; stipules green or purple, lance-ovate or broadly ovate and acuminate, or obtuse and dentate, serrate, ciliate; inflorescence long-peduncled, densely spicate, elongating more or less in anthesis, 3–7 cm. broad;

[13] Gray in Mem. Am. Acad. N. S. **4**: 19. 1849 (Pl. Fendl. 19. 1849).

bracts green or purplish, membranous, 2–12 mm. long, 2–15 mm. wide, deeply bifid, the lobes lanceolate, ovate, and acuminate, or obtuse and dentate, about 6 mm. wide, serrate and ciliate with long tawny hairs; calyx more or less tawny-hirsute at base and on the veins as well as finely stellate-pubescent (in interior region forms), the lobes purple-tipped, ovate-acuminate, membranous, serrate, and long-ciliate; petals purple, up to 2.5 cm. long; carpels often purple-tinged, glabrous and strongly striate-grooved dorsally (by obliteration of transverse nervations), and closely reticulate laterally.

Distribution: California, along the coast in wet places, Sonoma County, marshes of the Point Reyes Peninsula, Marin County, in the Great Central Valley, and in the foothills of the Sierra Nevadas from Shasta County to Mariposa County.

Specimens examined:

California: mendocino county—inland swamps, Pt. Arena, 11 July 1904, *Congdon* (M); sonoma county—Petaluma, May 1880, *Congdon* (C, S); Duncan's Mills, 17 June (18 July) 1882, *M. E. Jones* (CAS, G, M, P type, S, US); Valley Ford, 5 June 1886, *Curran* (OAC); Valley Ford, 5 June 1886, *K. Brandegee* (C); Valley Ford, 15 June 1886, *Curran* (S); June 1887, *Curran* (US); North Falls, Stewart's Canyon, May 1889, *M. S. Baker* (C); Santa Rosa, *K. Brandegee* (C); Stewart's Pt., 3 July 1920, *Abrams 7617* (S); marin county—4 June 1886, *Curran* (ND, S); near Lake Lagunitas, June 1895, *Merrill* (G, US); Pt. Reyes, 18 June 1900, *Jepson 1174* (M cotype of *S. rhizomata* Jepson); Point Reyes, 18 June 1900, *Davy 6730* (C); Point Reyes (Post Office), July 1903, *Elmer 4936* (C, CAS, M, P, S, US); Lake Lagunitas, 11 May 1918, *Eastwood* (CAS); San Anselmo Canyon, April 1922, *Sutliffe* (CAS, P); Pt. Reyes, 13 May 1923, *Eastwood* (CAS); north of Lake Lagunitas, 8 May 1927, *J. T. Howell 2365* (CAS); napa county—near Napa City, April 1896, *Sonne* (F, ND); sacramento county—upper road between Fair Oaks and Folsom, 20 April 1918, *Hannibal* (S); near Sacramento, 2 April 1915, *Philips* (S); san joaquin county—near Stockton, April 1923, *Steinbeck* (CAS); shasta county—Welch's, 6 July 1898, *M. S. Baker 493* (C); butte county—adobe flats or swales, April 1896, *Austin 132* (M); Iron Canyon, May 1896, *Austin 132*

(US); Chico, March 1897, *Bruce 1923* (P); May 1897, *Austin* (US); Little Chico Canyon, 29 June 1905, *Krautter 62* (G); Table Mountain, Olive Ranch, north of Oroville, 23 May 1912, *A. A. Heller 10751* in part (ANSP, C, F, G, M); Clear Creek schoolhouse, in the *Quercus Douglasii* belt, 8 May 1914, *A. A. Heller 11381* (ANSP, C, CAS, G, M, OAC, S, US); 8 miles north of Oroville, 23 March 1914, *A. A. Heller 11225* (ANSP, CAS, G, M, OAC, S, US); ELDORADO COUNTY—May 1884, *Curran* (G, probably authentic material for *S. sulcata* Curran); Simpson's Ranch, Sweetwater Creek, 29 May 1907, *K. Brandegee* (C, P, S, US); AMADOR COUNTY—Ione, 1886, *K. Brandegee* (C); Stoney Creek, 1000 ft. alt., 26 May 1896, *Hansen 1671* (M, ND, P, S, US); CALAVERAS COUNTY—Salt Springs Valley, 19 May 1921, *Tracy 5645* (C); TUOLUMNE COUNTY—Chinese, 330 m. alt., 22 May 1913, *Eggleston 9101* (US); MARIPOSA COUNTY—White Rock, 17 April 1892, *Congdon* (G); below Mormon Bar, 15 June 1902, *Congdon* (S, US); Lewis, 17 April 1892, *Congdon* (S).

Sidalcea calycosa and *S. sulcata* have been combined, separated, then recombined in a most bewildering manner. *Sidalcea rhizomata* is a more recent segregate from this group. However, from the large number of specimens examined, it is shown that these three "species" are essentially the same in leaves, bracts, pubescence, inflorescence, and fruit. They are also similar in habit, since some of the most delicately slender specimens from the foothills of the Sierra Nevada exhibit a tendency toward the rhizomatously rooting condition displayed by those nearer the coast, and often show some degree of succulency, especially in the basal leaves. A gradual transition can be traced from the slender and often much branched plants of the dry interior region to those of the moister regions near the coast. This transition seems to be only a matter of degree and involves an increase in the tendency toward succulency, a more congested inflorescence, longer hairs, and larger and more dentate or cleft bracts. Plants collected by *M. K. Curran* (*K. Brandegee*) at Valley Ford, 5 June 1886, as well as by *M. E. Jones* (US Herb. *No. 11840*, cotype of *S. calycosa*) are intermediate between *S. calycosa* of Jones and *S. rhizomata* of Jepson. *Elmer No. 4936* from the Point Reyes post-office is only slightly more succulent

and rhizomatous than *Philips* (S Herb. *No. 67026*) collection from Sacramento County. *A. A. Heller No. 11225* from Butte County and *Hansen No. 1671* from Amador County show a decided tendency toward rooting along the decumbent portion of the stem, with larger floral parts, more congested inflorescence, and thickened leaves.

After critical examination of the characters given above, it was thought best to reduce *S. sulcata* and *S. rhizomata* to synonymy and consider the very succulent plants of the Point Reyes peninsula as only an *ecad* of the subsaline (or saline) marshes. In the future should transplant experiments prove this supposition to be incorrect, then the members of this very characteristic group with the sulcate carpels will again have to be treated as distinct entities.

4. **S. Hartwegi** Gray in Benth. Pl. Hartw. 300. 1848; in Mem. Am. Acad. N. S. **4**: 20. 1849 (Pl. Fendl. 20. 1849); Walp. Ann. **2**: 151. 1851–52; Brew. & Wats. Bot. Calif. **1**: 83. 1876, as to name only; Gray in Proc. Am. Acad. **21**: 409. 1886; Greene, Fl. Francis. 103. 1891; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 29. 1894); Gray, Syn. Fl. N. Am. **1**[1]: 303. 1897; Jepson, Fl. West. Mid. Calif. 239. 1901, and ed. 2. 259. 1911; Man. Fl. Pl. Calif. 628. 1925. Pl. 6, fig. 2.

S. tenella Greene in Bull. Calif. Acad. Sci. **1**: 7. 1884; *ibid.* 79. 1885.

S. Hartwegi var. *tenella* Gray in Proc. Am. Acad. **22**: 286. 1887; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 29. 1894); Gray, Syn. Fl. N. Am. **1**[1]: 304. 1897.

Annual from a slight tap-root; stems erect, up to 4 dm. high, slender, simple, and strict, or slightly to much branched, glabrescent or minutely stellate-pubescent; leaves palmately or pedately 5–7-parted into linear, entire or 2–3-lobed segments, up to 6 cm. broad, sparsely short-stellate on the lower surface, almost glabrous on the upper surface; basal leaves merely lobed, small, and early deciduous; inflorescence racemose, few-flowered; rhachis, pedicels, bracts, and calyx rather closely stellate-pubescent; bracts short, merely bidentate or shortly bifid; calyx deeply cleft, lobes lanceolate or ovate, long-acuminate, sparsely ciliate;

petals rose-purple, retuse; carpels glabrous, favosely rugose-reticulate.

Stamineal column slender, the outer series of phalanges closely approximate to the inner at the summit, more or less united into pairs as in the perennial species; anthers abortive or wanting in the pistillate flowers.

Distribution: dry hillsides in the Sierra Nevada foothills of California from Shasta County to Mariposa County, in the Sacramento Valley, and in the coastal region from Mendocino County to San Francisco County.

Specimens examined:

CALIFORNIA: SHASTA COUNTY—Burney, 17 June 1923, *Bethel* (CAS); BUTTE COUNTY—Chico, May 1878, *Bidwell* (ANSP); Little Chico, June 1883, *Austin* (G TYPE of *S. Hartwegi* var. *tenella* Gray, ND); Chico, 1883, *Parry* (M); Chico, 27–28 April 1885, *Gray* (C); Clear Creek, 15–30 April 1897, *Brown 193½* (ANSP, F, M, S, US); Forest Ranch, 3 May 1897, *Austin 1873* (US); Forest Ranch, May 1897, *Bruce 1873* (P); plains, May 1887, *Bruce 1922* (P); plains, March 1897, *Austin 1922* (US); mountain gorges, May 1898, *Bruce 2389* (P); Berry Canyon, near Clear Creek, 9 May 1902, *Heller & Brown 5212* (ANSP, F, G, M, P, S, US); 2 miles from Chico, 16 April 1914, *A. A. Heller 11298* (CAS, F, G, M, ND, OAC, S, US); hills 8 miles north of Oroville, 11 May 1914, *A. A. Heller* (G, M, S); ten miles north of Chico, 15 April 1917, *A. A. Heller 12675* (ANSP, CAS, F, G, M, OAC, S, US); Richardson Springs road, 5 miles from Chico, 28 April 1926, *A. A. Heller 13934* (US); near Little Chico Creek, 7 May 1927, *A. A. Heller 14366* (ANSP); YUBA COUNTY—Brownsville, 1880, *Hill* (M); Los Vergils, 22 May 1921, *Eastwood 10516* (CAS, G); NEVADA COUNTY—22 miles east of Marysville, 11 May 1911, *W. W. Jones 133* (G); Nevada City, 20–22 June 1912, *Eastwood 602* (CAS, G, M); near Grass Valley, 25 May 1919, *A. A. Heller 13198* (ANSP, CAS, F, G, M, S, US); PLACER COUNTY—Auburn, May 1878, *Austin 11467* (G, M); Auburn, 1882, *Ames* (ANSP); Colfax, 3 July 1882, *M. E. Jones* (P); Auburn, May 1891, *Ames* (P); Palm Avenue, Auburn, April 1895, *Ames* (US); Rose Springs, 28 May 1926, *Bacigalupi, McMunn & Mason 1499* (S); ELDORADO COUNTY—Coloma, 30 May 1901, *Rix-*

ford (G, US); Sweetwater Creek, 15 May 1907, *K. Brandegee* (ANSP, M, P, US); without locality, *Curran* (G); AMADOR COUNTY—New York Falls, 2000 ft. alt., April 1893, *Hansen 507* (M, S); Clinton, 2000 ft. alt., 1 June 1894, *Hansen 507* (US); New York Falls, 1500 ft. alt., 2 June 1894, *Hansen 508* (US); Agr. Station, May 1892, *Hansen* (M, S); CALAVERAS COUNTY—Reservoir, 18 May 1887, *B. H. Smith* (ANSP); near Wallace, about 300 ft. alt., 7 May 1927, *Stanford 220* (CP, OAC); near Burson, about 500 ft. alt., 12 May 1928, *Stanford 1005* (CP); Mokelumne Hill, *Blaisdell* (CAS, US); TUOLUMNE COUNTY—near French Flat, 1300 ft. alt., 25 April 1919, *W. J. Williamson 12* (CAS, CP, P, S, US); MARIPOSA COUNTY—Aqua Tria, April 1880, *Congdon* (G); summer of 1880, *Hollick* (US); April–June 1883, *Congdon* (US); Whitlocks, 20 May 1893, *Congdon* (S); Lewis, 25 April 1895, *Congdon* (S); Stockton Creek, 18 May 1902, *Congdon* (US); 1914, *Faunt le Roy* (CAS); Blockman's Ranch, April 1915, *Eastwood* (CAS, G, US); FRESNO COUNTY—Base Camp, junction n. and s. forks King's River, 10 April 1923, *W. B. Duncan* (S); MENDOCINO COUNTY—Potter Valley, 19 May 1928, *Eastwood 12665* (CAS, P); SONOMA COUNTY—Sonoma Creek, 10 May 1885, *Rattan* (S); COLUSA COUNTY—Stony Creek, June 1884, *Rattan 21* (G, S); LAKE COUNTY—Lower Lake, 1 June 1893, *Blankinship* (G); Scott's Valley, 6 miles northwest of Lakeport, 1400–2000 ft. alt., 28 May–2 June 1902, *Tracy 1648* (US); near Lakeport, 12 May 1903, *C. F. Baker 2963* (CAS, G, M, ND, P, US); Lakeport, 16 May 1917, *Bentley* (S); NAPA COUNTY—Napa Valley, 1853–4, *Bigelow* (ANSP, G); Calistoga, 18—, *Parry* (M); west of Oakville, 12 May 1895, *Greene* (ND); White Sulphur Spr., St Helena, 8 May 1907, *Chandler 7567* (C); SOLANO COUNTY—Hartley's, 6 May 1930, *C. F. Baker 2877* (CAS, F, G, M, ND, P, US); SACRAMENTO COUNTY—Folsom, May 1883, *Curran* (OAC); SAN JOAQUIN COUNTY—Tracy, 25 April 1903, *C. F. Baker 2869* (ND); Clements, 7 May 1927, *Stanford 219* (CP, P); WITHOUT LOCALITY—*Hartweg 1669* (G TYPE); 1853–4, *Bigelow* (ANSP, US); 1882, *Parry* (US); 189–, *Austin 132a* (M); Central Pacific Railroad, May–June 1884, *A. H. Smith* (ANSP).

Brewer and Watson[14] in the 'Botany of California' inadvert-

[14] Brew. & Wats. Bot. Calif. 1: 83. 1876.

ently combined the two annual species, *S. Hartwegi* and *S. hirsuta* under the former name. Dr. E. L. Greene,[15] unaware of this error, described specimens of *S. Hartwegi* under the name of *S. tenella*, retaining the name of *S. Hartwegi* for those plants which rightfully belong to *S. hirsuta*. In 'Flora Franciscana'[16] he reduced *S. tenella* to synonymy under *S. Hartwegi*. Dr. Gray[17] noted that the *S. tenella* of Greene was only a depauperate form of *S. Hartwegi* with much-reduced flowers and aborted anthers; nevertheless, he[18] later designated it *S. Hartwegi* var. *tenella*. The specimen in question is one collected by Mrs. Austin in the gravelly bed of Little Chico Creek, Butte County, and is merely a much-attenuate and pale form of the pistillate plant of true *S. Hartwegi*, and therefore not worthy of varietal rank. Although many plants of this species are very slender, others are much branched and have light-colored or even white flowers. Some forms of *S. Hartwegi* may easily be confused with *S. calycosa* of the Central Valley region but the carpels of *S. calycosa* have the long deep sulcations on the dorsal surface, whereas those of *S. Hartwegi* are rugulose. The two are often collected together and have been confused in herbaria. If the carpels are immature then the stamineal column must be used for specific differentiation, since *S. Hartwegi* has the narrow phalanges of the perennials instead of the broad petaloid ones of the annuals.

Section 2. Perennes Roush

2. Perennes Roush, new section

Perennials from a creeping rootstock, or a strong variously thickened woody root, mostly summer-flowering, leafy-stemmed or scapiform; basal, middle cauline, and upper cauline leaves strikingly different (rarely similar) as to lobing or segmentation; the outer stamineal phalanges evident, closely approximate to the inner terminal ones, narrow and bifid, each lobe diantheriferous (except in *S. pedata*); carpels variously marked dorsally or smooth. Sp. 5–18.

[15] Greene in Bull. Calif. Acad. Sci. **1**: 7. 1884; *ibid.* 79. 1885.
[16] Greene, Fl. Francis. 103. 1891.
[17] Gray in Proc. Am. Acad. **21**: 210. 1886.
[18] Gray, Syn. Fl. N. Am. **1**[1]: 303. 1897.

KEY TO THE SPECIES

a. Stems usually erect and leafy; basal leaves lobed, not parted; basal and cauline leaves dissimilar.
  b. Plants mostly glabrous; carpels mostly smooth.
    c. Inflorescence a close raceme; flowers white or yellowish; plants of the Rocky Mountains.................................*5. S. candida*
    cc. Inflorescence an elongated raceme; flowers deep purple; plants of the ciscascade region from coastal British Columbia to midwest Oregon...*6. S. Hendersoni*
  bb. Plants more or less pubescent; carpels mostly reticulate.
    c. Inflorescence spiciform; pedicels mostly short.
      d. Plants mostly hirsute at the base; inflorescence densely spicate. ....*7. S. spicata*
      dd. Plants with a soft silky pubescence; inflorescence shortly or interruptedly spicate; plants of Tulare County, California........ ....*7a. S. spicata* var. *ranunculacea*
      ddd. Plants harshly puberulent, occasionally glabrescent; inflorescence elongated, spiciform; plants of the northern Great Basin extending to central Oregon.........................*8. S. oregana*
      dddd. Plants harshly puberulent; inflorescence shortly spiciform; plants of the Umpqua Valley, Oregon..........*8a. S. oregana* var. *Cusickii*
    cc. Inflorescence racemose; pedicels mostly long.
      d. Flowers light rose to almost white....................*9. S. campestris*
      dd. Flowers purple, rarely white in *S. neo-mexicana*.
        e. Plants densely and softly stellate-pubescent; raceme loose, virgate..*10. S. virgata*
        ee. Plants slightly hirsute to stellate-pubescent; raceme dense, not virgate.
          f. Stems with few long hairs; inland species......*11. S. neo-mexicana*
          ff. Stems glabrous and more or less glaucous; plants of southern California.................*11a. S. neo-mexicana* var. *parviflora*
          fff. Stems with short stellate pubescence; plants of Inyo County, California....................*11b. S. neo-mexicana* var. *Covillei*
        eee. Plants with mixed hirsute and stellate pubescence; raceme loose, not virgate.
          f. Stems decumbent to suberect, not rooting at the nodes; coastal species.
            g. Leaves hirsute, or sparsely stellate-pubescent; common coastal species.........................*12. S. malvaeflora*
            gg. Leaves with a soft, stellate tomentum; plants of the Santa Inez Mts. and from near Santa Barbara, California.... ....*12a. S. malvaeflora* var. *californica*
          ff. Stems decumbent, rooting at the nodes; montane species.... ....*13. S. reptans*
aa. Stems ascending to suberect, mostly leafy; basal leaves lobed to parted; basal and cauline leaves similar (except in *S. robusta*).
  b. Stems erect, or laxly procumbent, slender, not glaucous, stellate-pubescent (often somewhat scurfy) throughout........*14. S. asprella*

bb. Stems erect, stout, somewhat glaucous, glabrescent; plants of Butte County, California .... *15. S. robusta*

bbb. Stems procumbent, rarely erect, slender, glaucous, glabrous or stellate-puberulent .... *16. S. glaucescens*

aaa. Stems usually caespitose-ascending, somewhat leafy to scapiform; basal leaves parted; basal and cauline leaves dissimilar.

b. Plants caespitose and glaucous; flowers large, deep purple; plants of western Nevada .... *17. S. multifida*

bb. Plants scapose and hirsute; flowers small, rose-purple; plants of Bear Valley, San Bernardino County, California .... *18. S. pedata*

5. **S. candida** Gray in Mem. Am. Acad. N. S. **4**: 20, 24. 1849 (Pl. Fendl. 20, 24. 1849); Gen. Ill. **2**: 58. *pl. 120, f. 9.* 1849; Walp. Ann. **2**: 151. 1851–52; Torr. & Gray in Pacif. R. R. Rept. **2**: 126. *pl. 2.* 1855; Wats. Bot. King Exp. 46. 1871; Porter, Fl. Colo. 16. 1874; Garden **24**: 396. *text-fig.* 1883; *ibid.* **28**: 29. *text-fig.* 1885; Greene in Bull. Calif. Acad. Sci. **1**: 74. 1885; Coulter, Man. Bot. Rocky Mt. 41. 1885; Gray in Proc. Am. Acad. **22**: 286. 1887; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 30. 1894); Rev. Hort. **63**: 356. *text-fig.* 1891; Gray, Syn. Fl. N. Am. **1**^{1}: 304. 1897; L. H. Bailey in Bailey, Cyc. Am. Hort. **4**: 1667. 1902; Jour. Hort. III, **56**: 451. *text-fig.* 1908; Nelson in Coulter & Nelson, Man. Bot. Cent. Rocky Mt. 317. 1909; Hubbard in Bailey, Stand. Cyc. Hort. **6**: 3162. *f. 3615.* 1917; Rydb. Fl. Rocky Mts. 558. 1917, and ed. 2. 558. 1922; Bailey, Man. Cult. Pl. 486. 1924.

Pl. 5, figs. 3 and 5; pl. 8, fig. 1.

S. candida var. *tincta* Cockerell in Bot. Gaz. **29**: 280. 1900.

Perennial from a slender creeping rootstock; stem erect, 4–9 dm. high, simple, strict, mostly glabrous and leafy up to the inflorescence; leaves thin, ciliate, the upper surface glabrous, the lower with few stiff hairs on the veins; basal leaves orbicular, 4–15 cm. broad, about 7-lobed, the lobes coarsely and obtusely dentate, sinus truncate; middle cauline leaves 5–20 cm. broad, cut more than half-way to the base, segments 2–3-dentate at apex; upper cauline leaves 4–10 cm. broad, parted into 1–7 somewhat lance-linear and mostly entire segments; stipules ovate, ciliate; inflorescence terminal, racemose, densely flowered, 7–10 cm. long, 3 cm. broad; rhachis, pedicels, and calyx densely stellate-pubescent; bracts broadly lanceolate or ovate, ciliate;

calyx-lobes broadly deltoid, margin ciliate and veins pubescent; petals obovate, emarginate, 10–15 mm. long, white or yellowish (rarely pink-tinted); anthers blue (rarely pink before dehiscence); carpels 7–9, smoothish or slightly reticulate, glabrous except at the minutely hairy apex.

Distribution: along mountain streams in the Rocky Mountains from southern Wyoming to New Mexico and west to Utah and Nevada.

Specimens examined:

Wyoming: Cummins, 28 July 1895, *A. Nelson 1489* (G, M, US); Centennial Valley, 9 June 1895, *A. Nelson 1296* (G); Centennial, Albany Co., 6 Aug. 1900, *A. Nelson 7967* (G, M, P, US); Chimney Park, 1 Aug. 1901, *E. Nelson 651* (G); Copperton, alt. 8700 ft., 6 Aug. 1901, *Tweedy 4569* (US); Centennial, Albany Co., 2 Sept. 1903, *Goodding 2120* (G, M, US).

Colorado: without locality, 1862, *Hall & Harbour 85* (ANSP, F, G, M); Middle Park, Aug. 1862, *Parry 429* (G, M); without locality, 1864, *Parry 85 (1862)* (US); Rocky Mts., 1868, *Vasey 89* (M, US); Breckenridge, Rocky Mts., 1871, *T. S. Brandegee 124* (C, M); Eagle River, 20 Aug. 1873, *J. M. Coulter* (ANSP, F, G); Middle Park, near Hot Springs, 9000 ft. alt., 29 July 1874, *E. A. Barber* (US); Crestone, Sangre de Cristo, 9500 ft. alt., Sept. 1877, *T. S. Brandegee* (C); Hot Sulphur Springs, Middle Park, 13 Aug. 1884, *C. S. Sheldon 211* (US); Cameron Pass, 1888, *Cassidy* (F); Gunnison, July 1888, *Eastwood 12* (US); Breckenridge, 1888, *Wislizenus 841* (M); Cameron Pass, 10,000 ft. alt., 7 Sept. 1890, *Crandall 201* (P); Cameron Pass, 10,000 ft. alt., 7 Sept. 1890, *Crandall* (US); Cameron Pass, 9800 ft. alt., 7 Sept. 1890, *Crandall 81* (US); Michigan Hill, Cameron Pass, 9500 ft. alt., 7 Sept. 1890, *Crandall 107* (G); Surface Creek, Delta Co., 6100 ft. alt., July 1892, *Purpus 230* (F); Hotchkiss, 22 June 1892, *Cowen* (SCW); Pagosa Springs, 7000 ft. alt., 20 July 1893, *B. H. Smith* (ANSP); mountains of Larimer Co., Aug. 1893, *Osterhout* (W); near Steamboat Springs, 7000 ft. alt., 16 July 1894, *C. F. Baker* (P); Telluride, 10,500 ft. alt., 20 Aug. 1894, *Tweedy 134* (US); Wolcott, Eagle Co., 11 July 1896, *Biltmore Herb. 3486a (Colo. Exped. 1–684)* (G, US); LaVeta, 14 July 1896, *Shear 3638* (US); on Grizzly Creek, 8000 ft. alt., 24 July 1896, *C. F. Baker*

(M); Estes Park, 18 July 1897, *Osterhout* (M, US); foothills above Dix, 10 July 1898, *M. E. Jones 679* (G, M, P); McCoy, 30 July 1898, *Shear & Bessey 5305* (US); Red Dirt Divide, 31 July 1898, *Shear & Bessey 3968* (US); foothills above Dix, 10 July 1898, *Baker, Earle & Tracy 679* (G, M, P, US); Piedra, 14 July 1899, *C. F. Baker* (P); near Breckenridge, Summit Co., 9700 ft. alt., Aug. 1901, *Mackenzie 101* (M, US); Gunnison, 7680 ft. alt., 31 July 1901, *C. F. Baker 670* (M, P, US); Rogers, 14 Aug. 1901, *C. F. Baker 800* (C, G, M, P, US); Williams Fork, Routt Co., 27 July 1903, *Sturgis* (C, G); Steamboat Springs, 20 July 1903, *Goodding* (US); Baxter Pass, Book Plateau, Routt Co., 8500 ft. alt., 22 Sept. 1906, *Cary 116* (US); Eldora, 8600 ft. alt., 28 July 1906, *Daniels 162* (M); vicinity of Mount Carbon, Gunnison Co., 2730 m. alt., 6 July 1910, *Eggleston 5868* (US); north of Tomichi Dome, Gunnison Co., 2700 ft. alt., 18 Aug. 1911, *Marsh 7739* (US); Paradox Creek, Montrose Co., 7500 ft. alt., 20 July 1912, *E. P. Walker 323* (G); Tabegauche Basin, 8000 ft. alt., 21 July 1913, *Payson 138* (G, S); Tabegauche Basin, 8000 ft. alt., 20 Aug. 1913, *Payson 192* (G, F, M); Dillon, Summit Co., 2670 m. alt., 13–14 Sept. 1915, *Eggleston 11958a* (US); Eldora, Boulder Co., 8800 ft. alt., 6 Aug. 1918, *Clokey 3175* (G, M, P, S); Tolland, 8900 ft. alt., 2 Aug. 1919, *Munz 3186* (P); Rocky Mts., *Vasey* (M); without locality, *Purpus 243* (C); base of Palisade Mts., near Brook, Larimer Co., 11 Aug. 1929, *Woodson 1814* (M).

NEW MEXICO: *Fremont's Expedition to California*, 1845–7 (*410*, 1845) (ANSP, G, US); 1847, *Fendler 80* (ANSP, G TYPE, M, US); Piedra Parada, 20 July 1859, *Newberry* (US); northern New Mexico, 1867, *Parry 23* (M); mountains near Las Vegas, July 1881, *Vasey* (US); Hermit Peak, Aug. 1882, *Snow* (C, M, US); along Ruidoso Creek, in the White Mountains, Lincoln Co., 6600 ft. alt., 1 July 1895, *Wooton* (US); Comanche Valley, 8500 ft. alt., July 1896, *St. John* (G); Pecos River (Pews River), Truchas Peak, 17 July 1898, *Coghill 69* (M, US); Harvey's Ranch near Las Vegas, 1899, *Cockerell* (G, US COTYPE of *S. candida* var. *tincta* Cockerell); Harvey's Ranch near Las Vegas, 1899, *Beschle* (G); Silver Springs Cañon, 6 July 1899, *Wooton* (M, US); head of Pecos River, 8000 ft. alt., 17 July 1903, *V. Bailey 552a* (US);

Sandia Mountains, 23 July 1903, *Hedgcock* (M); mouth of Ponchuelo Creek, 8400 ft. alt., 30 June 1908, *Standley 4077* (G, M, US); vicinity of Chama, Rio Arriba Co., 2380–3850 m. alt., 8 July 1911, *Standley 6588* (US); Bartlett Ranch, Colfax Co., 4 Sept. 1913, *Wooton* (US); Balsam Park, Sandia Mountains, 8200 ft. alt., 10 Aug. 1914, *Ellis 214* (M, US); vicinity of Brazos Canyon, Rio Arriba Co., 31 Aug. 1914, *Standley & Bollman 10969* (US); southeast of Cuba, 8300 ft. alt., 30 July 1915, *Read 17* (US); vicinity of Ute Park, Colfax Co., 2200–2900 m. alt., 30 Aug. 1916, *Standley 14062* (US); Cloudcroft, Aug. 1920, *Schulz 289* (P).

Utah: Wasatch Mts., 6000 ft. alt., July 1869, *Watson 194* (G, US); Beaver City, 1877, *Palmer 62* (G, M, US); Park City, 8000 ft. alt., 18 Aug. 1881, *M. E. Jones 2139* (P, S); Elk Ranch, 7000 ft. alt., 12 Sept. 1894, *M. E. Jones 6039f* (P, US); La Sal Mts., 7000–8000 ft. alt., Aug. 1899, *Purpus 6697* (C, M, P, US); Parley's Park, 28 Aug. 1901, *M. E. Jones* (P); Fish Lake, around Twin Creeks, 8 Aug. 1905, *Rydberg & Carlton 7486, 7610* (G, US); Gogorza, Summit Co., about 6350 ft. alt., 11 Aug. 1908, *Garrett 2287* (Gar., G); Parley's Park, Kimball's, Summit Co., 19 July 1909, *C. P. Smith 1876* (F, S); Holiday Park, Uinta Mts., 14 Aug. 1911, *Mrs. J. Clemens* (P); Elk Mountains, near Scorup's Camp, 2500 ft. alt., 8 Aug. 1911, *Rydberg & Garrett 9528* (Gar., M); Gooseberry Ranger Station, Fishlake National Forest, Wasatch Mountains, Sevier Co., 2400 m. alt., 3 Aug. 1914, *Eggleston 10372* (US); Salina Experiment Station, Fishlake Forest, Wasatch Mountains, Sevier Co., 2400 m. alt., 28–29 Aug. 1915, *Eggleston 11716* (US).

Nevada: Muncy, 2 July 1891, *A. J. Jones* (M).

This species is unlike any other in the genus, being the most distinct in the leaf-form, almost entirely lacking in pubescence, except in the inflorescence, usually having single terminal racemes and large, whitish or yellowish flowers with blue anthers (pink in some specimens). Its habitat along streams in the high Rockies may account for the glabrous condition. Although often cultivated, there are many forms in cultivation under this name that are more nearly related to *S. neo-mexicana* but pass under the name of *S. malvaeflora*, an older untenable name for *S. neo-*

mexicana. Once the characters of *S. candida* are known there is no possibility of its being confused with any other species.

Sidalcea candida var. *tincta* Cockerell is only a local color form of the species.

6. **S. Hendersoni** Wats. in Proc. Am. Acad. **23**: 262. 1888; E. G. Baker in Jour. Bot. **29**: 52. 1891 (Synopsis Malveae, 31. 1894); Gray, Syn. Fl. N. Am. **1**[1]: 306. 1897; Howell, Fl. N. W. Am. 101. 1897; Piper, Contr. U. S. Nat. Herb. **11**: 388. 1906; Piper & Beattie, Fl. N. W. Coast, 238. 1915.

S. malvaeflora var. *Oregana* Watson acc. to Macoun, Cat. Can. Pl. **3**: 501. 1886.

S. malvaeflora Gray acc. to Macoun, Cat. Can. Pl. **5**: 313. 1890.

Perennial from a woody root, glabrous or nearly so throughout; stem erect, stout, mostly simple, up to 12 dm. high; basal leaves orbicular, 5–7-lobed, the lobes crenate or dentate, ciliate; middle cauline leaves up to 12 cm. broad, cleft more than half-way, the lobes or segments broad and coarsely dentate, sparsely pubescent on the upper surface or only on the veins, ciliate; the upper cauline leaves 3–5-parted into narrow, coarsely dentate segments; stipules often purplish, lanceolate or linear, acute; inflorescence purplish, elongate, densely or laxly racemose; rhachis and bracts sparsely stellate, pedicels and lower part of calyx more densely stellate-pubescent; bracts purplish, mostly simple, of about equal length with the pedicel, somewhat scarious and ciliate; calyx large, accrescent, reticulate-veined, lobes purple-tipped, rarely green, ovate and abruptly acute or acuminate, glabrous or nearly so, ciliate; petals drying a deep purple, emarginate; carpels grayish, 7 or 8, smooth and glabrous, the apiculation slender, persistent.

Distribution: in marshes near the sea, Vancouver Island, British Columbia, Washington, Oregon, and small islands along the coast.

Specimens examined:

Canada:

British Columbia: Victoria, 1883, *Meehan* (ANSP); near Victoria, May 1885, *Fletcher* (G); Oak Bay, Vancouver Island,

June 1887, *Macoun* (US); Vancouver Island, 21 July 1893, *Macoun 53* (G, ND); Alberni, vicinity of Victoria, 1 July 1908, *Macoun* (F); Vancouver Island, July 1915, *Carter* (G); Alberni, Vancouver Island, July 1916, *Carter 376* (G); Lower Fraser Valley, 20 Sept. 1917, *Henry* (S).

United States:

Washington: Satchop (Satsop) River, 1838–42, *Wilkes Expl. Exp. 206* (US); Seattle, 9 July 1889, *Piper 723* (G, ND, W, probably cultivated specimens); Seattle, 15 July 1892, *Mosier* (US); mouth of Snohomish River, near Everett, July–Sept. 1895, *Claypool* (SCW); Whidby Island, 20 June 1897, *Gardner* (C, SCW, W); Hoquiam, 29 June 1897, *Lamb 1218* (M, S, SCW, US); Everett, 7 July 1904, *Piper 4915* (G, SCW, US); tide flats, Hoquiam & Aberdeen, 20 June 1908, *Foster 801* (US); San Juan Island, 14 July 1914, *Pope* (W); tideland, Marysville, July 1927, *J. M. Grant* (P).

Oregon: Saturna Island, 1858, *Lyall* (G); mouth of the Umpqua, 15 June 1887, *T. Howell 734* (G); near Clatsop Bay, 3 July 1887, *Henderson 1413* (G type); near Nestucca Bay, Aug. 1909, *Peck 6857* (Wil.); ½ mile north of Divide, 18 June 1919, *J. C. Nelson 2646* (G); Cottage Grove, Lane County, 1920, *M. S. Clemens* (US); Seaside, Clatsop Co., 11–12 July 1922, *Abrams 8917* (M, P, S, Wil.); south side of Sand Lake, 12 July 1924, *Peck 13420* (Wil.); Cannon Beach, Clatsop Co., 1 Aug. 1929, *Henderson 11360* (O).

Some of the collections cited in the 'Synoptical Flora'[19] under *S. glaucescens* prove to be *S. Hendersoni.* This restricts the range of the former to California and Nevada, leaving the distribution of the latter near the waters of Puget Sound and the rivers of the coastal counties extending to middle-western Oregon. Most of the plants of this species are practically glabrous except on the calyx-lobes. However, a collection by *Pope* (W. Herb. No. 1202) has long sparse hairs over its entire surface. The leaves have much the same form as those of *S. oregana* but, with the exception of the specimen cited, are bright green and glabrous. The inflorescence usually has a purplish tinge, although plants collected by *Henry* (S. Herb. No. 153110) show none of

[19] Gray, Syn. Fl. N. Am. 1[1]: 306. 1897.

this color, but are grayish-green throughout. The flowers are ordinarily deep purple, and even the calyx-lobes are typically, but not constantly, purple-tipped. The pistillate flowers are very small and appear different from those that are perfect. This is a very well-defined species and not closely related to any other of the Northwest.

7. **S. spicata** (Regel) Greene in Bull. Calif. Acad. Sci. **1**: 76. 1885; Gray in Proc. Am. Acad. **22**: 288. 1887; Greene, Fl. Francis. 104. 1891; E. G. Baker in Jour. Bot. **29**: 52. 1891 (Synopsis Malveae, 31. 1894); Gray, Syn. Fl. N. Am. **1**[1]: 306. 1897; Howell, Fl. N. W. Am. 101. 1897; H. M. Hall in Univ. Calif. Publ. Bot. **4**: 201. 1912; Hubbard in Bailey, Stand. Cyc. Hort. **6**: 3162. 1917; Smiley in Univ. Calif. Publ. Bot. **9**: 265. 1921; Jepson, Man. Fl. Pl. Calif. 629. 1925.

Pl. 6, fig. 5; pl. 10.

Callirhoe spicata Regel in Gartenfl. **21**: 291. *pl. 737*. 1872.

Sidalcea valida Greene in Pittonia **3**: 157. 1897.

S. hydrophila Heller in Muhlenbergia **1**: 107. 1904.

S. eximia Greene in Cyb. Columb. **1**: 34. 1914; Jepson, Man. Fl. Pl. Calif. 629. 1925.

S. Nelsoniana Piper in Proc. Biol. Soc. Wash. **32**: 41. 1919.

"*Sidalcea Murrayana*" in Gray, Syn. Fl. N. Am. **1**[1]: 306. 1897, in synonymy.

Perennial from a strong woody root; stem slender or stout, mostly erect, 2–10 dm. high, often paniculately branched above, usually hirsute on the lower portions, rarely puberulent; basal leaves orbicular, 1–10 cm. broad, crenate, slightly lobed, or more or less parted into usually 3-lobed segments, on hirsute petioles up to 4.5 dm. long, upper surface glabrescent, or variously pubescent, lower surface more or less hirsute, especially on the veins; middle cauline leaves about 7-cleft, the segments acutely 3–5-lobed or more coarsely dentate, pubescence chiefly on the veins of the lower surface; upper cauline leaves smaller, parted into 3–7 linear and entire, rarely coarsely dentate segments, glabrous or slightly pubescent; inflorescence more or less densely spicate, 1–30 cm. long, 0.5–4 cm. wide (often elongating in fruit); rhachis, bracts, and pedicels variously pubescent, corresponding to the

prevailing pubescence of stem and leaves; bracts often purple-tinged, linear, bifid, or subulate, merely ciliate, or hirsute; pedicels very short, slightly elongating after anthesis, glabrescent, hirsute, or stellate-puberulent; calyx very small, accrescent, glabrescent, closely stellate or strikingly hirsute; the lobes ovate, acute or acuminate, ciliate; petals varying from deep purple to a delicate rose-pink, small and narrow, erose or emarginate; carpels smooth or slightly reticulate.

Distribution: Lake Tahoe region of Nevada, northeastern and southwestern Oregon, and California along the coast to Sonoma County; the Coast Ranges to Napa County; and the Sierra Nevada to Mono County.

Specimens examined:

Nevada: Truckee Valley, 4000 ft. alt., July 1867, *W. W. Bailey 192* (US); Reno, 29 Aug. 1898, *Hillman* (P); about Washoe Lake, 1570 m. alt., 25 June 1902, *C. F. Baker 1168* (C, CAS, G, M, P, US); Washoe Lake, June 1902, *C. F. Baker* (P); Lake Tahoe, 6300 ft. alt., 5 Aug. 1906, *Kennedy 1420* (US); Little Valley, Washoe Co., 4 July 1907, *C. L. Brown* (ANSP, G); Franktown, 5000 ft. alt., 28 June 1909, *A. A. Heller 9781* (ANSP, G, F, S, US); summit above Glenbrook, June–Aug. 1911, *K. Brandegee* (C); Glenbrook, on Lake Tahoe, 1890 m. alt., 7 July 1919, *Tidestrom 10391* (US); south of Martelle Lake, 2010 m. alt., 8 July 1919, *Tidestrom 10441* (US).

Oregon: umatilla county—Meacham, July 1915, *Peck 6869* (Wil.); union county—above La Grande, 1 Aug. 1910, *Peck 6875* (Wil.); Hot Lake, 1 Aug. 1915, *Peck 6874* (Wil.); baker county—3 miles west of Whitney, 22 July 1921, *Peck 10351* (S); Sumpter, Blue Mts., 8 July 1919, *Ferris & Duthie 1062* (S); hood river county—Cloud Cap, Mt. Hood, summer 1929, *Van Dyke* (CAS); crook county—at Farewell Bend, 1270 m. alt., 18 July 1894, *Leiberg 483* (C, G, M, P, S, US); near the desert, 1897, *Cusick 1668* (C, G); Laidlaw, 19 July 1906, *Whited 3099* (O, OAC, US); deschutes county—Paulina Lake, 28 Aug., *Detling 281* (O); Bend, 27 July 1914, *Peck 6848* (Wil.); bank of Deschutes River, 15 mi. s. of Bend, 11 July 1925, *Peck 14314* (S); island in Deschutes River at Tumalo, 1 July 1921, *Whited 252* (S): Bend near Deschutes River, 1 Aug. 1922, *Abrams 9616*

(P, S); LAKE COUNTY—Crooked Creek, July 1886, *Austin* (C); Warner Range, 1700 m. alt., 25 June 1896, *Leiberg 2657* (O); Warner Range, 1700 m. alt., 25 July 1896, *Coville & Leiberg 45* (US); Warner Range, 1900 m. alt., 26 July 1896, *Coville & Leiberg 66* (US); Congon Peak, 1900 m. alt., *Coville & Leiberg 205* (US); about 10 miles south of Lakeview, 1450 m. alt., 19 June 1911, *Eggleston 7031* (US); Paisley, 4200–5000 ft. alt., Sept. 1914, *Elder 7* (US); near Paisley, 4200–5000 ft. alt., Sept. 1914, *Elder 70* (OAC); near Paisley, June 1915, *Elder 168* (OAC); Goose Lake Valley, near Lakeview, 28 June 1927, *Peck 15297* (M, S, Wil.); 35 miles northwest of Lakeview, 1 July 1927, *Peck 15406* (Wil.); 35 miles northwest of Lakeview, 1 July 1927, *Peck 15404* (S, Wil.); 35 miles northwest of Lakeview, 3 July 1927, *Peck 15443* (M, S, Wil.); KLAMATH COUNTY—Klamath Valley, 4200 ft. alt., *Cronkhite 82* (C, US); Buck Lake, 24 July 1897, *Coville & Applegate 37* (US); 3 Aug. 1897, *Austin & Bruce 1659* (P, US); Williamson River, July 1913, *Coombs* (CAS, G, US); Ashland, 14 July 1913, *Peck 6861* (Wil.); Fort Klamath, 16 July 1920, *Peck 9545* (G); 5 miles south of Beaver Marsh, 2–4 Aug. 1922, *Abrams 9676* (P, S); Beattie, 25 June 1927, *Peck 15205* (S, Wil.); Beattie, 25 June 1927, *Peck 15205a* (Wil.); High Cascades, 30 miles east of Medford, June 1927, *Heckner* (Wil.); Crater Lake Park, 6500 ft. alt., 9 Aug. 1929, *Wynd 1640* (O); HARNEY COUNTY—banks of Silvie's River in Bear Valley, 20 July 1898, *Cusick 2053* (C, F, G, M, ND, O, P, US); MARION COUNTY—Salem, *O. B. Johnson 243* (W); 1871, *E. Hall 71* (G, M); near Portland, 20 July 1881, *T. Howell 606* (G); Corvallis, 27 June 1916, *Gilbert 875* (OAC); Salem, 5 June 1916, *J. C. Nelson 650* (S, authentic material of *S. Nelsoniana* Piper); Salem, 12 June 1917, *J. C. Nelson 1294* (G); 3 miles south of Salem, 21 June 1919, *J. C. Nelson 2693* (S); 1 mile south of Salem, 23 June 1920, *J. C. Nelson 3155* (Wil.); Woodburn, 19 July 1920, *M. S. Clemens* (US); Salem, 11 June 1921, *J. C. Nelson 3843* (ANSP); ½ mile south of Salem, 2 July 1922, *J. C. Nelson 4368* (G); 1 mile south of Salem, 2 July 1922, *J. C. Nelson 4356* (OAC); 2½ miles north of Salem, 7 July 1922, *Abrams 8761* (P, S); TILLAMOOK COUNTY—Tillamook, 31 May 1892, *Owens* (OAC); CLATSOP COUNTY—Cannon Beach, 1 July 1924, *Peck 13224* (Wil.); Saddle

Mt., 3300 ft. alt., 10 June 1928, *Patterson 49* (O); DOUGLAS COUNTY—Glendale & Grant's Pass, 12 July 1887, *Henderson 151* (ANSP, O, S, OAC); Roseburg, Umpqua Valley, 26 June 1887, *T. Howell 1100* in part (M); JACKSON COUNTY—Ash Creek, July 1893, *Austin 4* (C); JOSEPHINE COUNTY—Takilma, 26–27 June 1912, *Peck 8029* (G, Wil.); Grant's Pass, 26 June 1886, *Henderson* (S); Grant's Pass, 20 May 1886, *Henderson* (S); Grant's Pass, June 1886, *Henderson* (G); Grant's Pass, 24 June 1909, *Peck 6863* (Wil.); Grant's Pass, 1909, *Peck 6871* (Wil.); base of Eight Dollar Mt., near Selma, 19 June 192–, *Henderson 7235* (O); near Eight Dollar Mt., near Selma, 20 June 1926, *Henderson 7234* (O); WITHOUT DEFINITE LOCALITY—Lake of the Woods, 14 Aug. 1896, *Gorman 443* (US); meadowland, 10 Aug. 1902, *Howard* (OAC); near Woodville, 1 July 1909, *Peck 6870* (Wil.); Woodruff Meadows, 2 July 1925, *R. A. Pendleton* (OAC).

CALIFORNIA: MODOC COUNTY—Forestdale, 1893, *M. S. Baker* (S); Davis Creek, July 1894, *Black* (ANSP); Lassen Creek, Aug. 1894, *Austin* (C); Parker Creek, 15 June 1919, *Ferris & Duthie 155* (RM, S); LASSEN COUNTY—Dixey Valley, 3 July, *M. S. Baker* (C); Susanville, 30 June 1892, *T. S. Brandegee* (C); Susanville Summit, 6000 ft. alt., 2 July 1897, *M. E. Jones* (P, US); 1 mile below Drakesbad, 5400 ft. alt., 24–26 Aug. 1925, *Cain 72* (S); PLUMAS COUNTY—29 July 189–, *Austin 1408* (US); Prattville, 3 July 1892, *T. S. Brandegee* (C); Prattville, 31 July 1920, *M. S. Clemens* (US); Prattville, 1906, *Coombs* (CAS); Portola, 1913, *K. Brandegee* (C); Gold Lake Region, Aug. 1917, *Sutliffe* (CAS); Salmon Lake, 1 Sept. 1920, *Sutliffe* (CAS); Drakesbad, 28 Aug. 1926, *M. S. Baker 338* (S); BUTTE COUNTY—Colby, July 1896, *Austin 209* (US); Chico Meadows, 4000 ft. alt., 6 Aug. 1914, *A. A. Heller 11645* (C, CAS, F, G, M, ND, OAC, S, US); Jonesville, 4000 ft. alt., 2 Aug. 1920, *H. F. Copeland 202* (S); Butte Meadows, 10 July 1928, *A. A. Heller 14650* (M); SIERRA COUNTY—Purdy, 1 July 1907, *Heller & Kennedy 8669* (ANSP, CAS, F, G, M, S, US); East Hot Springs, Sierra Valley, 27 Aug. 1909, *Dudley* (S); Loyalton, 29 June 1918, *Eastwood 7822* and *7821* (CAS); Salmon Lake, July 1918, *Sutliffe* (CAS); Salmon Lake, Oct. 1925, *Sutliffe* (CAS); Webber Lake, 6–12 Aug. 1927, *Haley* (CAS); NEVADA COUNTY—Soda Springs, 7000 ft. alt.,

21 July 1881, *M. E. Jones 2433* (P); Donner Park, 31 July 1887, *Sonne 342* (ANSP); Donner Park, Sept. 1888, *K. Brandegee* (C); Truckee, Aug. 1893, *Michener* (C); July 1897, *Blasdale* (C); Truckee, 16 July 1901, *Williamson* (ANSP); lower end of Donner Lake, 19 July 1903, *A. A. Heller 6898* (ANSP, C, F, G, M, P, S, US); July 1913, *K. Brandegee* (C); Truckee, 1750 m. alt., 14 July 1913, *A. E. Hitchcock 274* (US); Boca, July 1913, *K. Brandegee* (C); Cisco, 15 Aug. 1927, *A. A. Heller 14446* (O); PLACER COUNTY —Hot Springs, 11 July 1886, *Sonne 342* (S); Summit Station, Aug. 1888, *Greene* (G, M); Sierra Nevada Mts., Aug. 1892, *Carpenter* (C); Oct. 1892, *Carpenter* (C); Summit, 15 July 1908, *K. Brandegee* (C); ridge above Bear Valley, 7 July 1919, *V. Jones* (CAS); Cisco, 6000 ft. alt., 15 Aug. 1927 (ANSP, M); ELDORADO COUNTY—1866, *Rattan* (S); near Lake Tahoe, 6280 ft. alt., July 1899, *Hawthorne & Blaisdell* (CAS); Lake Tahoe, 27 July 1906, *Eastwood 1098a* (C); Fallen Leaf Lake, 27 July–15 Aug. 1906, *Eastwood 1098* (CAS); Deer Park Springs, Lake Tahoe, 1909, *Newcomer* (S); road to Glen Alpine Springs, 19 July 1909, *Lathrop* (S); Fallen Leaf Lake, 1923, *Lorraine* (S); LAKE TAHOE REGION—Lake Tahoe, 31 Aug. 1872, *Redfield 41* (M); 1890, *J. A. Sanford 419* (C); 1 Aug. 1891, *W. H. Evans* (M); meadow back of Tahoe City, 29 June 1900, *Dudley* (S); June 1900, *King* (G); Lake Tahoe, 25 June 1906, *G. B. Grant 7072* (C, P, S); Sunnyside, 1909, *Eastwood 62* (CAS, US); Lake Valley, 6400 ft. alt., 27 July 1911, *Abrams 4772* (C, G, P, S, US); near Lily Lake, 6600 ft. alt., 23 July 1913, *Smiley 325* (G); near Suzy Lake Trail from Glen Alpine, 7500 ft. alt., 18 July 1913, *Smiley 188* (G); Lake Tahoe, 6 Sept. 1920, *M. S. Clemens* (CAS); Lake Tahoe, Aug. 1920, *Keyes* (P); Hope Valley, 8500 ft. alt., Aug. 1892, *Hansen 505* (M, P, S); Hope Valley, 20 July 1918, *W. H. Evans* (C); MONO COUNTY—Mono Pass, 1866–67, *Bolander 6265* (M, G, US); Camp 125, near west branch of Walker's River, 15 July 1863, *Brewer 1860* (C, US); Summit, Aug. 1883, *Curran* (G); Walker Lake, 17 Aug. 1894, *Congdon 21* (G); Bloody Canyon, 20 July 1889, *Chesnut & Drew* (C); Walker Lake, 17 Aug. 1894, *Congdon* (C); Scott's Meadows, 21 Aug. 1898, *Congdon* (G); 26 Aug. 1908, *Minthorn* (C); meadow north of lake, Silver Lake, 7200 ft. alt., 26 June 1925, *Peirson 6107* (P); near pass between

east and west forks of Walker River, 13 Aug. 1925, *H. M. Hall 12136* (C); SISKIYOU COUNTY—Mount Shasta, 25 Aug. 1880, *G. Engelmann* (M); near Yreka, 23 June 1876, *Greene 885a* (G, M); Happy Camp, Klamath, June 1879, *Rattan* (S); Sisson's, Shasta Co., July 1887, *T. S. Brandegee* (C); Sisson's, July 1888, *T. S. Brandegee* (C); Mount Shasta and vicinity, 13–27 July 1892, *Palmer 2532* (US); near Sisson, 3550 ft. alt., 1–10 June 1897, *H. E. Brown 337* (ANSP, C, F, M, S, US); Medicine Lake, 7000 ft. alt., Aug. 1897, *M. S. Baker 148* (C); Shackleford Canyon, 6000 ft. alt., June 1901, *Chandler 1707* (C); Sisson, 13 Sept. 1902, *G. B. Grant* (S); Sisson, 12 Aug. 1903, *E. B. Copeland 3822* (C, G, M, P, US); foothills of Goosenest Mountain, 22 June 1909, *Butler 905* (C); Quartz Valley, 6 July 1910, *Butler 1643* (P); Oro Fino, 17 July 1910, *Butler 1728* (CAS, C, M, OAC, P); Sisson, 18 July 1912, *Eastwood 1216* (CAS, G, M, US); 20 June 1913, *L. E. Smith 383* (CAS, G, US); south fork of Shasta River, Mount Eddy, Shasta Forest, 1850–2000 m. alt., 11–12 Aug. 1915, *Eggleston 11656* (US); Bray, July 1915, *L. E. Smith* (CAS); near Wagon Creek Falls, 20 July 1916, *A. A. Heller 12474* (ANSP, CAS, F, G, M, OAC, S, US); Castle Lake, 24 July 1921, *Eastwood 10766* (CAS); Medicine Lake, 28 July 1921, *Eastwood 10964* (CAS, G); in Shasta Valley, between Edgewood and Gazelle, 23 June 1928, *A. A. Heller 14647* (M); SHASTA COUNTY—Great Spring, Hat Creek, 4500 ft. alt., June 1903, *Hall & Babcock 4272* (C); Jason & Stewart's Camp, headwaters of Hat Creek, 2120 m. alt., 31 July–1 Aug. 1911, *Eggleston 7420* (US); TRINITY COUNTY—Union Creek, 4250 ft. alt., July 1909, *H. M. Hall 8688* (C); LAKE COUNTY—summit of Elk Mt., July–Aug. 1892, *Jepson* (C); Snow Mountain, 3700 ft. alt., 23 Aug. 1892, *T. S. Brandegee* (C); Webber Lake, 5 July 1901, *Kennedy & Doten 109* (C); near Hullville on the ridge between Eel River and Rice Creek, 11 Aug. 1902, *A. A. Heller 6047* (ANSP, G, M, P, US, COTYPES of *S. hydrophila* Heller); mountains of northern Lake County, Sept. 1902, *Mackie* (C); Elk Mountain, 4000–5000 ft. alt., 21 July–16 Aug. 1905, *Tracy 2288* (C); Elk Mountain, 4000–5000 ft. alt., 21 July–16 Aug. 1905, *Tracy 2351* (C); north slope of Elk Mountain, 25 July 1913, *H. M. Hall 9586* (C, US); NAPA COUNTY—Angwin's, Howell Mountain, 24 Sept. 1893, *Jepson* (C);

HUMBOLDT COUNTY—valley of Elk River, region about Humboldt Bay, 0–500 ft. alt., 25 June 1907, *Tracy 2578* (C, G, M, RM, S, US TYPE of *S. eximia* Greene); Murphy Meadow, Bald Mountain, 3500 ft. alt., 1 Sept. 1917, *Tracy 4831* (C, P); Trinity Summit, 5000 ft. alt., 18 Sept. 1919, *Tracy 5253* (C); Dow's Prairie, 200 ft. alt., 25 July 1920, *Tracy 5344* (C, CAS, P); Dow's Prairie, 200 ft. alt., 29 Aug. 1920, *Tracy 5394* (C); Trinity Summit, Elk Horn Prairie, 5000 ft. alt., 16 Aug. 1925, *Kildale 1188* (S); MENDOCINO COUNTY—Sherwood, 14–16 July 1915, *A. S. Hitchcock* (US); SONOMA COUNTY—Knight's Valley, June 1894, *Greene* (ND TYPE of *S. valida* Greene); Knight's Valley, Aug. 1894, *Booth* (ND authentic material of *S. valida* Greene); Kenwood, 19 July 1927, *M. S. Baker 2343* (S); Kenwood, 29 July 1928, *M. S. Baker 3203c* (C); WITHOUT LOCALITY—May–Oct. 1898, *Purpus* (C); Paynes Spring, 1 Aug. 1898, *M. S. Baker 493* (ANSP); 1877, *Vasey* (US); Sierra Nevada, 1887, *Parry* (M); Morgans Springs, 22–26 Aug. 1912, *Eastwood 1888* (CAS, M, US); Howell Mountain, Aug. 1888, *T. S. Brandegee* (C); Chat, 5300 ft. alt., 21 June 1897, *M. E. Jones* (P); 7 miles from French Meadows, 18 Aug. 1901, *Kennedy & Doten 411* (C, S); Gray Eagle Meadows, Feather River Region, 6000 ft. alt., 13 July 1920, *Head* (CAS); Prospect Peak, summer 1929, *Kramer* (CAS); Cahto, July 1869, *Kellogg & Harford 110* in part (US); Mt. Shasta, Sept. 1902, *Grant 5216a* (C).

When Dr. Greene[20] described his *S. spicata* from collections by Dr. Kellogg at Cisco, California, and by Mrs. Curran near Donner Lake, he said: "It may or may not be the *Callirhoe spicata* of Regel, neither the figure of which, nor any description, has been accessible to me, but no other Sidalcea has its racemes condensed into the appearance of a short spike, if we except the annual species at the end of this synopsis." Regel's[21] description applies more exactly to those less hirsute forms in the Sierra Nevada of California and in Oregon as being "basi hirsuta, caeterum glabriuscula," whereas Greene's description "equably hispid-hirsute throughout" applies not only to many of the plants of the Sierra Nevada region but especially well to those

[20] Greene in Bull. Calif. Acad. Sci. **1**: 76. 1885.

[21] Regel in Gartenfl. **21**: 291. *pl. 737*. 1872.

of the coastal areas (*S. eximia* Greene[22]). The figure of Regel's plant[21] shows it to be very similar to *S. hydrophila* Heller[23] from Lake County, California (*Heller No. 6047*) except for the length of the inflorescence; and it is not unlike *S. Nelsoniana* of Piper from near Salem, Oregon. *Sidalcea valida* Greene of Sonoma County is merely a paniculately branched form of *S. spicata*, with fewer hirsute hairs and more densely stellate pubescence.

It has seemed inadvisable to recognize all the species previously described in the *S. spicata* group. The type specimens are distinct but the intermediate forms are so numerous that no distinct and clear-cut lines can be drawn. Tracy considered his number *2578* (type of *S. eximia* Greene) from Humboldt County as merely a much more vigorous plant than those of the mountains. Since the flora of Humboldt County is conceded to be almost tropical in luxuriance, this robust and very hirsute form may be due to the habitat. All gradations of hirsuteness and leaf-form may be encountered as one passes from the coast region through Siskiyou and Trinity Counties to the Sierras, or in passing north into Oregon by way of Grant's Pass. The inflorescence varies from an extremely short glomerulate spike to a very long loose spike. The calyces are all small. The petals are large in the broadly spicate forms but extremely small in the pistillate flowers of the slender delicate spikes of the form described as *S. Nelsoniana* Piper. The carpels for the most part are smooth, though slight nervations may be found in some plants of drier habitats. The leaves, although mostly basal, in the more robust forms may continue to the inflorescence; and the lobes may be very coarsely dentate. There are indications in the specimens examined that a slight difference in the amount of available moisture (both soil and atmospheric) may make a great difference in the degree and kind of pubescence in this species.

7a. Var. **ranunculacea** (Greene) Roush, n. comb.
S. ranunculacea Greene, Leafl. Bot. Obs. **1**: 75. 1904.
S. interrupta Greene, *ibid.*
Rootstock horizontal; leaves gray-green, silky villous-hirsute,

[22] Greene in Cyb. Columb. **1**: 34. 1914.
[23] Heller in Muhlenbergia **1**: 107. 1904.

ciliate; inflorescence a short, more or less interrupted spike, elongating after anthesis; rhachis, bracts, pedicels, and calyx densely stellate-pubescent with some long hairs intermixed, appearing villous-hirsute; carpels obviously though not strongly reticulated.

Distribution: mountains of Tulare, Kern, and San Bernardino Counties, California.

Specimens examined:

CALIFORNIA: KERN COUNTY—Greenhorn Mts., 1 June 1926, *Weston 167* (CAS); TULARE COUNTY—above Hockett's meadow, 2 Aug. 1904, *C. F. Baker 4318* (Coll. *Culbertson*) (CAS, C, G, M, P TYPE OF *S. ranunculacea*); Natural Bridge Meadow, 8000 ft. alt., 9 Aug. 1904, *C. F. Baker 4255* (Coll. *Culbertson*) (CAS, G, M, P TYPE of *S. interrupta*); Natural Bridge of Volcano Creek, July 1904, *Hall & Babcock 5434* (C, S); Fish Creek, 8000 ft. alt., June 1904, *Hall & Babcock 5208* (C); Bonita Meadow, 8000 ft. alt., 20–24 June 1904, *Hall & Babcock 5176* (C); Giant Forest, Aug. 1905, *K. Brandegee* (C); north side of Toowa Range, 9000 ft. alt., 20 July 1908, *Hall & Hall 8404* (C); Clicks Creek, basin of Little Kern River, 6600 ft. alt., 15 July 1908, *Hall & Hall 8372a, b* (ANSP, C); Hossack Creek, 6500 ft. alt., 13 July 1908, *Hall & Hall 8362* (C); marshes, Sequoia National Park, July 1908, *Davidson 1716* (S); north fork of Middle Fork Tule River, 7500 ft. alt., 5 Aug. 1908, *Hall & Hall 8481* (C); Pine Flat, near Cal. Hot Springs, 2 June 1917, *Moxley 586* (C); vicinity of Mt. Moses, 6500 ft. alt., Sept. 1923, *Duncan* (S); Long Meadow, 8000–9000 ft. alt., 7–14 June 1888, *Palmer 203* (ND, M, US); Halsted Meadows, Sequoia National Park, 2150 m. alt., 8 Aug. 1891, *Coville & Funston 2103* (US); about 1½ miles below Mineral King, Sierra Nevada, 2700 m. alt., 4 Aug. 1891, *Coville & Funston 1462* (US); Mineral King, 27 July 1892, *T. S. Brandegee* (C); Kern River Valley, Tobias Meadow border, 16 July 1895, *Dudley 598* (S); borders Summer Home Meadow, region of Middle Tule River, 28 July 1895, *Dudley 914, 915* (S); above Pond Meadow, by small lake, Upper Kaweah River, 22 Aug. 1896, *Dudley 1721* (S); between Brook's Camp and Lone Pine, Upper Kaweah River, 22 Aug. 1896, *Dudley 1722* (S); near Middle Tule River, 8000–9000 ft. alt., April–Sept. 1897, *Purpus 5184* (C, G,

M, US); below Soda Spring, 6500–7500 ft. alt., 17 July 1897, *Dudley 1963* (S); Soda Spring, 6200 ft. alt., 28 July 1897, *Dudley 2303* (S); below Kern Kaweah Falls, 6000–8000 ft. alt., 31 July 1897, *Dudley 2350* (S); Lake of Islands vicinity, region of Kaweah Peaks, 11000–13000 ft. alt., 2 Aug. 1897, *Dudley 2392* (S); Mineral King, 8000 ft. alt., 22 Aug. 1899, *E. B. Copeland 23* (US); Thorpes Meadow, Giant Forest, 3 Aug. 1900, *Dudley 3013* (S); Round Meadow, Sequoia National Park, 13 July 1902, *G. B. Grant 1974* (S); Caboon Meadow, 9 July 1902, *Dudley* (S); SAN BERNARDINO COUNTY—Mare Flats, 8000 ft. alt., 8 July, *Crawford* (P); Seven Oaks Camp, San Bernardino Mts., 5000 ft. alt., June 1901, *G. B. Grant 1201* (C); on the Sierras between Alta Meadow and Sequoia, 28 Aug. 1917, *Munz 1555* (P); City Creek Grade, San Bernardino, 24 June 1926, *M. E. Jones* (P).

The peculiar form of inflorescence, the silky-villous hirsuteness of the leaves, and the more reticulate carpels, as well as the geographical range, separate this from the species sufficiently for varietal distinction.

8. **S. oregana** (Nutt.) Gray in Mem. Am. Acad. N. S. **4:** 20. 1849 (Pl. Fendl. 20. 1849), in part; Greene in Bull. Calif. Acad. Sci. **1:** 77. 1885; Gray in Proc. Am. Acad. **22:** 287. 1887; Macoun, Cat. Can. Pl. **5:** 313. 1890, as to name only; Greene, Fl. Francis. 104. 1891, in part; E. G. Baker in Jour. Bot. **29:** 52. 1891 (Synopsis Malveae, 30. 1894), not as to Canadian plants; Greene, Man. Bay-Region Bot. 65. 1894; Gray, Syn. Fl. N. Am. **1**[1]: 305. 1897; Howell, Fl. N. W. Am. 102. 1897; Jepson, Fl. West. Mid. Calif. 240. 1901, and ed. 2. 260. 1911; Piper in Contr. U. S. Nat. Herb. **11:** 388. 1906; Hubbard in Bailey, Stand. Cyc. Hort. **6:** 3162. 1917; Rydb. Fl. Rocky Mts. 558. 1917, and ed. 2. 558. 1922; Jepson, Man. Fl. Pl. Calif. 628. 1925. Pl. 6, fig. 6; pl. 9.

Sida oregana Nutt. in Torr. & Gray, Fl. N. Am. **1:** 234. 1838; Walp. Rep. **1:** 316. 1842.

Sidalcea malvaeflora Gray in Brew. & Wats. Bot. Calif. **1:** 84. 1876, in footnote.

S. malvaeflora Gray var. *Oregana* Watson acc. to Macoun, Cat. Can. Pl. **3:** 501. 1886, as to synonymy only.

S. nervata A. Nels. in Proc. Biol. Soc. Wash. **17**: 94. 1904; Nelson in Coult. & Nelson, Man. Bot. Cent. Rocky Mt. 317. 1909; Rydb. Fl. Rocky Mts. 558. 1917, and ed. 2. 558. 1922; Tidestrom in Contr. U. S. Nat. Herb. **25**: 353. 1925.

S. campestris Greene acc. to Rydb. Fl. Rocky Mts. 558. 1917, and ed. 2. 558. 1922, as to name only.

Perennial from a woody root, mostly stellate-puberulent throughout; stems solitary or few, simple or paniculately branched, erect, up to 15 dm. high, often glabrous below but puberulent toward the inflorescence; leaves large, coarse, strongly nerved below, harsh with a dense stellate pubescence, particularly on the lower surface; basal leaves orbicular or reniform, up to 10 cm. broad, about 8-lobed, the lobes cuneate, 2–3-dentate, petioles as much as 30 cm. long; middle cauline leaves 5–7-parted, the cuneate, lanceolate, or linear segments incisely tri-dentate or more deeply cleft; upper cauline leaves pedately parted into 3–5 linear, mostly entire segments; inflorescence a more or less elongated spiciform raceme, often reaching a length of 30 cm., singly or paniculately disposed; rhachis, bracts, pedicels, and calyx rather densely puberulent; bracts linear or subulate, rarely bidentate or bifid; calyx-lobes ovate-lanceolate, acute, or shortly acuminate; petals of the perfect flowers rose-purple, obovate, emarginate, 1–2 cm. long, those of the pistillate flowers a third smaller and of deeper color; carpels smoothish or lightly reticulated.

Distribution: roadsides, moist meadows, and along streams, southwest Montana to Utah, west to southeastern Washington and northern California.

Specimens examined:

Montana: Middle Creek Canyon, Gallatin Co., 31 July 1902, *W. W. Jones* (G); Chisholm Camp, 6500 ft. alt., 31 July 1902, *Blankinship* (C, G); Middle Temperate Life Zone, 3000 ft. alt., 19 July 1909, *M. E. Jones* (C, M, P, S).

Wyoming: near Ft. Bridger, Aug. 1892, *Leidy* (ANSP, US); Evanston, 14 July 1883, *J. A. Sanford* (C, ND); La Barge, Uinta Co., 15 July 1894, *Stevenson 119* (US); Evanston, 27 July 1897, *A. Nelson 4101* (RM TYPE of *S. nervata* A. Nels.); Evanston, 10 July 1897, *Williams* (CAS, US).

Idaho: Boise City, June 1881, *Wilcox* (G); July 1889, *Sandberg* (F, US); June–July 1892, *Aiton 62* (M); Palouse Country, June–July 1892, *Aiton 1344* (M); 15 miles south of Moscow, 14 June 1892, *Sandberg, MacDougal & Heller 391* (C, G, M, P, S, US); near Julietta, Latah Co., 13 June 1892, *A. A. Heller 391* (ANSP); June 1892, *Sandberg* (C); Lake Waha, Aug. 1894, *Leiberg* (O); Curlew Gulch, 28 June 1892, *Mulford* (M); Moscow & Camas Prairie, 27 June, 24 July, 5 Sept. 1894, *Henderson* (US); forks of St. Mary's River, 950 m. alt., 3 July 1895, *Leiberg 1140* (C, F, G, M, O, US); s. w. corner of Big Camas Prairie, 5000 ft. alt., 14 July 1895, *Henderson 3106* (O, US); Lake Waha, Nez Perces Co., 2500–3000 ft. alt., 19 June 1896, *Heller & Heller 3260* (C, F, M, S, US); Mann's Creek, Washington Co., 2200 ft. alt., *M. E. Jones 6208* (P, M); Salubria, 10 July 1899, *M. E. Jones 6207* (P, RM, S, US); near Moscow, 18–24 July 1899, *Henderson* (S); Moscow, Latah Co., June 1900, *Abrams 732* (C, P); Big Willow, Canyon Co., 3000 ft. alt., 31 May 1910, *Macbride 165* (G, M, RM, SCW, US); Saw-tooth National Forest, Hailey, 1910, *Woods 335* (RM); Saw-tooth National Forest, 1910, *Woods 2621* (RM); Silver City, Owyhee Co., 7000 ft. alt., 18 July 1910, *Macbride 412* (M, RM); Ketchum, Blaine Co., 5887 ft. alt., 20 July 1911, *Nelson & Macbride 1204* (G, M, S, RM); Payette National Forest, 21 July 1911, *Miles* (US); Payette Forest, 21 July 1911, *Miles 172* (RM); Tamarack, 4 Aug. 1911, *J. A. Clark 185* (C, S, US); Dry Buck, Boise Co., 16 Aug. 1911, *Macbride 1639* (C, G, M, P, RM, S, SCW, US); near Boise, 1916, *Gageby* (RM); Camas Prairie, Blaine Co., 15 Aug. 1916, *Macbride & Payson 3807* (C, CAS, G, M, P, RM, S, US); along Palouse River, 10 Oct. 1922, *Cramer* (S); Thatuna Hills, 6 July 1926, *Epling & Houck 9186* (M, UCLA); Pierce to Oxford, 31 July 1926, *Epling & Houck 9652* (UCLA); Thatuna Hills, 6 July 1926, *Epling & Houck 9187* (M, UCLA); 3000 ft. alt., 8 Aug. 1925, *Epling & Offord 8777* (UCLA); 24 Aug. 1925, *Epling & Offord 8775* (UCLA); Partridge Meadow, July 1929, *Epling* (UCLA); Weippe, July 1929, *Epling* (UCLA); Santa, July 1929, *Epling* (UCLA); Partridge Meadow, near Elk River, July 1929, *Epling* (UCLA).

Utah: Deer Creek, 3 Aug. 1880, *M. E. Jones* (P); Timpanogos Peak, 21 Aug. 1889, *H. Engelmann* (M); Soldier Summit, 7300

ft. alt., 5 July 1894, *M. E. Jones 5597* (C, M, P, RM, US); American Fork Canyon, 7000 ft. alt., 15 July 1895, *M. E. Jones* (P); American Fork Canyon, 6 July 1895, *H. Jones* (S); Mendon, 17 June 1898, *Mulford 116* (M); Bear River, 7000 ft. alt., 26 July–2 Aug. 1902, *Pammel & Blackwood 4111* (G, M); Red Butte Canyon, Salt Lake Co., 22 June 1904, *Garrett 1014* (RM); north of Salt Lake City, 12 June 1905, *Rydberg 6169* (RM); Red Butte Canyon, Salt Lake Co., 12 July 1906, *Garrett 1853* (S, US); Gogorza, Summit Co., 11 Aug. 1908, *Garrett 2289* (Gar.); Paradise, Cache Co., 4 July 1909, *C. P. Smith 1742* (RM, S); Red Butte Canyon, Salt Lake City, 21 July 1909, *C. P. Smith 1901* (RM); Uinta National Forest, 7800 ft. alt., 30 July 1913, *Bowen 13* (RM); Salt Lake Co., 1920, *Garrett 540* (Gar.); Fish Lake Forest, 2360 m. alt., 29 July 1915, *C. D. Marsh 12330* (US); Aspen Grove, Wasatch Mts., 4 Aug. 1925, *Garrett 3410* (Gar.); meadow south of Soldier Summit, Utah Co., 7300 ft. alt., 19 Aug. 1929, *Garrett 5434* (Gar.).

NEVADA: Little Lake Canyon, Elko Co., *Kennedy 564* (M, RM); East Humboldt Mts., 14 July 1902, *M. E. Jones* (P); Palisade, 500 ft. alt., 17 June 1903, *Stokes* (US); Eureka, Eureka Co., 2 July 1904, *Kennedy 837* (RM); Big Creek, Lander Co., 6000 ft. alt., 26 July 1913, *Kennedy 4529* (ANSP, S); Mahoney Range station, 1911, *Garrison 37* (US); Gold Creek, 6300 ft. alt., 24 July 1912, *Nelson & Macbride 2104* (G, M, RM, US); Lone Mountain, Elko County, 7500 ft. alt., 5 Aug. 1913, *Kennedy 435* (S); Gold Creek, Elko Co., 7150 ft. alt., 7 Aug. 1913, *Kennedy 4395* (S).

WASHINGTON: 1882, *T. S. Brandegee* (C); 1883, *T. S. Brandegee 690* (ANSP); Falcon Valley, 20 July 1886, *Suksdorf* (G); Falcon Valley, 16 June 1890, *Suksdorf 2446* (G); 1889, *Vasey 223* (G, US); Yakima Co., June 1892, *Henderson 2436* (G, SCW); west Klickitat Co., 1500 ft. alt., 6 July 1892, *Suksdorf 2447* (G); Coulee City, Douglas Co., 10 July 1892, *Henderson 2433* (G, W); Union Flat, Whitman Co., 18–27 July 1892, *Hull 428* (G, SCW); Union Flat, Whitman Co., 18 July 1892, *Henderson 2437* (W); Icicle Creek, 430 m. alt., 25 July 1893, *Sandberg & Leiberg 586* (ANSP, C, CAS, F, G, M, US); Peshastin, 420 m. alt., 25 July 1893, *Leiberg 586* (O, SCW); Pullman, 5 Aug. 1893,

Piper 1644 (G, SCW, US, W); Pullman, 5 Aug. 1893, *Piper 1645* (F, G, US, W); Pullman, 21 July 1894, *Piper* (US); Skamania Co., 3000 ft. alt., 21 July 1894, *Suksdorf 2448* (G); mountain valley, Klickitat Co., 14 Sept. 1894, *Suksdorf 2449* (G); Whitman Co., 26 July 1896, *Elmer 321* (C, M, ND, P, US); Blue Mts., Waitsburg, 18 July 1896, *Piper 2396* (SCW); Academy Campus, 31 May 1897, *Horner 106* (C); Waitsburg, 31 May 1897, *Horner 115* (US); Waitsburg, 31 May 1897, *Horner 106B* (G); Ellenburg, 14 June 1897, *Whited 486* (M, SCW, US); Pullman, July 1897, *Elmer 1346* (P); Cow Creek, June 1902, *Griffiths & Cotton 534* (SCW, US); northeast Kittitas Co., 10 July 1903, *Cotton 1330* (SCW, US); Wenatchee Mts., Kittitas Co., 21 July 1904, *Cotton 1652* (G, SCW, US); Pullman, Whitman Co., 17 July 1919, *Ferris & Duthie 1246* (S); Leavenworth, 3 July 1904, *Whited 2559* (OAC); Pullman, 23 June 1925, *Eastwood, 13151* (CAS); on road from Moscow to Pullman near Holland, 28 June 1925, *Eastwood 13390* (CAS); Pullman, 24 June 1925, *Eastwood 13171* (CAS).

Oregon: Clear Water, *Spalding* (G, US); Klamath Valley, 4200 ft. alt., *Cronkhite 61* (C, US); near Corvallis, 31 May 1892, *Mulford* (M); Blue Mountains, Grant Co., 5150 ft. alt., 14 July 1896, *Coville 578* (US); near Beulah, Malheur Co., 1080 m. alt., 17 June 1896, *Leiberg 2300* (C, G, P, US); Swan Lake Valley, 28 June 1896, *Applegate 58* (G, US); Lake Co., 2 Aug. 1897, *Austin 1660* (US); Crow Creek, Wallowa Co., 4300 ft. alt., 29 June 1897, *E. P. Sheldon 8423* (G, M, US); common in moist bottoms, 25 July 1898, *Cusick 2165* (G); Klamath Valley, 25 June 1902, *Cusick 2831* (C, G, M, O, P, S, US); Billy Meadows, 5000 ft. alt., 15 July 1908, *Jardine 310* (US); Pendleton, 3 June 1910, *A. A. Heller 10172* (ANSP, G, M, S, US); in timber, edge of Cherry Creek Camp, 23 July 1910, *Rose 1713* (M); La Grande, 28 July 1910, *Peck 1415* (Wil.); wet meadows, Burns, 17 June 1912, *Peck 6860* (Wil.); Cabin Ranger district, Ochoco Forest, Blue Mountains, Crook Co., 1000 m. alt., 19–21 July 1915, *Eggleston 11388* (US); La Zinka Ranch, 20 mi. n. Ukiah, Umatilla Co., 1000 m. alt., 23, 24 June 1916, *Eggleston 12698, 127249* (US), Blue Mts., n. of Albee, Umatilla Co., 4000 ft. alt., 25 July 1917, *Lawrence 818* (US); Graham Creek, vicinity of Blue

Mts. Hot Springs, Grant Co., 4 July 1919, *Ferris & Duthie 843* (S); marshes, John Day River, Prairie City, Grant Co., 1 July 1919, *Ferris & Duthie 720* (S); meadow, Keno, Klamath Co., 6 July 1920, *Peck 9331* (G, M, Wil.); De Moss Springs, Sherman Co., 29 June 1921, *Peck 13308* (Wil.); 1 mile south of Antelope, Wasco Co., 28–30 July 1922, *Abrams 9560* (S); 6 miles south of Ft. Klamath, 2–4 Aug. 1922, *Abrams 9748* (S, P); Butte Creek below Fossil, Wheeler Co., 25 June 1925, *Henderson 5402* (CAS, G, M); Austin Ranch, E. Grant Co., 21 July 1925, *Henderson 5631* (CAS, M, S, Wil.); lower flanks of Stein's Mts., Alvord Ranch, Harney Co., 8 June 1927, *Henderson 8862* (CAS, O); Belle A Ranch, near Burns, Harney Co., 22 June 1927, *Henderson 8858* (CAS); Klamath Falls, 22 June 1927, *Peck 15128* (Wil.); Dairy Creek, 35 mi. n. w. of Lakeview, 1 July 1927, *Peck 15408* (S, Wil.); near Burns, Harney Co., 13 July 1927, *Henderson 8856* (CAS, O); near Burns, Harney Co., 13 July 1927, *Henderson 8857* (CAS); marshy meadow near Beatty, 7 July 1928, *Constance 9685* (O); near Pendleton, Umatilla Co., 24 June 1927, *Gabrielson* (M); WITHOUT LOCALITY—25 July 1898, *Cusick 2165* (C, G, M, US); 1887, *Cusick 1456* (US); Pine Creek, July 1898, *Austin & Bruce 2205* (C); Bingham Springs, western Blue Mts., 7 Oct. 1908, *Cusick* (M).

CALIFORNIA: *T. S. Brandegee* (C); common about Yreka, 23 June 1876, *Greene 885* (G, M); Mt. Shasta and vicinity, Siskiyou Co., 13–23 July 1892; *Palmer 2532* (C); Davis Creek, Modoc Co., Aug. 1894, *Black 67* (S); 1894, *Austin* (C); Goose Lake Valley, Aug. 1895, *Austin 417* (P); Eagle Lake, 27 miles from Susanville, 5000 ft. alt., 30 June 1897, *M. E. Jones* (P); fields, Goose Lake Valley, July 1898, *Austin & Bruce 2205* (C); near Yreka, 4 June 1909, *Butler 768* (C, P, S); dry land near Yreka, 26 May 1910, *Butler 1408* (C, P, RM, S, US); Parker Creek near Modoc National Forest Boundary, Warner Mts., Modoc Co., 15 June 1919, *Ferris & Duthie 35* (S); Parker Creek, Warner Mts., 15 June 1919, *Ferris & Duthie 154* (S); Kelseyville, Lake Co., 3 July 1924, *Blankinship* (CAS); Cedarville Road, Warner Mts., Modoc Co., 25 June 1926, *Peirson 6867* (P).

Although the type of *Sida oregana* Nutt. from "West side of Rocky Mts." was not seen, his *Sida heterophylla* seems to be

Sidalcea campestris, and may account for the confusion of these two Oregon species by some authors. In the absence of the type, if the original description be compared with the northern forms occurring west of the Rocky Mountains to the Willamette Valley in Oregon, the degree of pubescence ("glabrous" to "harsh puberulent," with no hirsute hairs), the elongated spiciform inflorescence, shape of calyx lobes, and size of flowers would indicate that *Sidalcea oregana* is polymorphic. Evidently the gynodioecism and gynodimorphism present is rather misleading as to flower size and color (as is true in all species that show this tendency). If it be borne in mind that the species *S. campestris,* as well as *S. virgata* of Howell, is restricted to the Willamette Valley, there seems to be little reason for confusing *S. oregana* and *S. campestris.* All those forms occurring in northern California, eastern Oregon, Idaho, Wyoming, Montana, and Nevada may be considered as the polymorphic *S. oregana.* Farther east the form of *S. nervata* A. Nelson, with a tendency toward the glabrous condition and larger and fewer flowers, seems to predominate. The more harsh form with denser but not smaller flowers is more frequent in eastern Oregon and Idaho. There is such an intergradation between the two that it seems best to treat all these as the form Nuttall had in mind in giving the locality of his *Sida oregana.*

The specimens cited by Macoun as *Sidalcea malvaeflora* var. *Oregana* Wats. acc. to Macoun are conspecific with *S. Hendersoni.*

8a. Var. **Cusickii** (Piper) Roush, n. comb.

Sidalcea Cusickii Piper in Proc. Biol. Soc. Wash. **29**: 99. 1916.

Scabrous-puberulent throughout; inflorescence more congested than that of the species; calyx turbinate, becoming campanulate at maturity, the lobes oblong-ovate, acute (apparently slightly constricted at the base), strongly nervose and puberulent; carpels slightly reticulate with very close short meshes.

Distribution: Umpqua Valley, Oregon.

Specimens examined:

Oregon: Roseburg, Umpqua Valley, 26 June 1887, *T. Howell* (*1100* in part) (M, ND, OAC); Umpqua Valley, 25 June 1887, *T. Howell 735* (G); Looking Glass, Umpqua Valley, 27 June

1887, *T. Howell* (*1101*) (OAC, M, ND, US); Umpqua Valley, 20 June 1887, *T. Howell 732* (G); Glendale, May 1887, *T. Howell* (C); Calopooya, Douglas Co., 800 ft. alt., 24 July 1899, *M. A. Barber 80* (G); along Antelope Creek, Jackson Co., 1800 ft. alt., 4 June 1898, *Applegate 2386* (RM); west of Crater Lake, 1 Aug. 1916, *Peck 6867* (Wil.); Roseburg, 22 June 1916, *Peck 6868* (Wil.); Sutherlin, Douglas Co., 19 June 1916, *Peck 6851* (Wil.).

This variety is decidedly different from other sidalceas in possessing a conspicuously campanulate calyx. It shows its relationship to *S. oregana* in most characters, although in leaf condition and fruiting racemes it also resembles cultivated forms of *S. campestris*.

9. S. campestris Greene in Bull. Calif. Acad. Sci. **1**: 76. 1885; Gray in Proc. Am. Acad. **22**: 286. 1887; E. G. Baker in Jour. Bot. **29**:52. 1891 (Synopsis Malveae, 29. 1894); Gray, Syn. Fl. N. Am. **1**^{1}: 305. 1897; Howell, Fl. N. W. Am. 102. 1897; Piper & Beattie, Fl. N. W. Coast, 238. 1915; Gilkey, Spring Fl. N. W. Oregon, 88. 1929. Pl. 8, fig. 2.

Sida malvaeflora Lindl. in Bot. Reg. **12**: 1036, *pl. 1036*. 1826; Torr. & Gray, Fl. N. Am. 234. 1838, not of DC.; Hook. Fl. Bor.-Am. **1**: 108. 1840, not of DC.

Sidalcea oregana Gray in Mem. Am. Acad. N. S. **4**: 20. 1849 (Pl. Fendl. 20. 1849), in part.

S. asplenifolia Greene in Pittonia **3**: 158. 1897.

S. sylvestris A. Nels. in Proc. Biol. Soc. Wash. **20**: 36. 1907.

Perennial from a woody root; stem erect, up to 18 dm. high, slender, or slightly branched, usually bristly hirsute with mostly two-rayed hairs, up to the inflorescence; basal leaves orbicular, 7–9-lobed, lobes 2–5-dentate at apex; hairs of the upper surface simple or geminate and appressed, those of the lower surface geminate or multiradiate, dense but not harsh or only slightly so; petioles up to 2 dm. long, retrorsely hirsute; middle cauline leaves up to 2.5 dm. broad, palmately parted almost to the base into 7–9 linear or somewhat cuneate coarsely serrate-pinnatifid segments; upper cauline leaves almost completely parted into 3–5–7 linear, entire or slightly dentate segments, either glabrescent or with few hairs on the veins on the lower surface, and

ciliate; inflorescence loosely racemose, 1–3.5 dm. long, long-pedicellate, cinereous stellate-pubescent throughout, generally hirsute also; bracts narrow, bifid and densely stellate; calyx-lobes often dull purplish, ovate-lanceolate, densely stellate, with long hairs at least on the margins; petals pale rose or whitish, about one-half smaller in the pistillate flowers than in the perfect flowers; carpels rugose or favosely reticulate, retaining their pubescence until almost mature.

Distribution: Willamette Valley, Oregon.

Specimens examined:

Oregon: Columbia River, *Nuttall* (ANSP); *Nuttall* (G); 1826 (?), *Douglas* (G probably authentic material of *Sida malvaeflora* Lindl.); Oregon City, 1868–9, *Kellogg & Harford 109* (G); Washington Co., July 1877, *T. Howell* (M); dry prairies, July 1880, *Eggert* (M); dry prairies, July 1881, *T. Howell 614* (G cotype, US); dry prairies, July 1881, *T. Howell* (US); Hood River, 26 June 1882, *Henderson 24* (G); Hood River, Wasco Co., July 1883, *Henderson 12* (G); Tualatin plains, July 1883, *Henderson 13* (G); Tualatin plains, July 1886, *Henderson 25* (G); Salem, 9 July 1887, *Henderson 150* (OAC, S); near Portland, 28 June 1888, *Henderson* (O); McMinnville, 20 July 1899, *Shear 5622* (US); Hillsboro, May 1889, *Gorman* (F, W); near Milwaukie, Multnomah Co., 15 July 1893, *Suksdorf 2216* (G); Gladstone, July 1894, *T. Howell 1492* (C, M, SCW, US); Corvallis, 29 June 1894, *Finley* (OAC); Corvallis, 26 May 1898, *Kincaid* (SCW); Portland, 13 July 1902, *E. P. Sheldon 10872* (G, M, O, P, SCW, US); along Willamette River, Wheatland, Yamhill Co., 17 July 1903, *Lunell* (RM); Portland, 7 July 1903, *Lunell* (US); Wheatland, Yamhill Co., 8 July 1903, *Lunell* (RM Herb. No. 52562 type of *S. sylvestris* A. Nels.); Salem, 21 April 1910, *Peck 6873* (Wil.); Salem, May 1911, *Peck 6872* (Wil.); Salem, June 1911, *Peck 6874* (Wil.); Salem, Aug. 1911, *Peck 6862* (Wil.); 1 mile north of Corvallis, 17 June 1912, *Walls & Owens* (OAC); near Gresham, near Portland, 11 July 1912, *Suksdorf 1877* (G); hills west of Salem, May 1913, *Peck 6855* (Wil.); hills west of Salem, May 1913, *Peck 6856* (W); Corvallis, 26 June 1913, *Gilbert 877* (OAC); Crabtree, 1915, *Hatch* (OAC); Salem, 16 May 1916, *J. C. Nelson 584, 585* (S); Salem, 7 June 1916, *J. C. Nelson 658* (S);

Salem, 12 June 1917, *J. C. Nelson 1302* (G); Portland, 29 June 1917, *Gorman 4124* (S); near Corvallis, 12 April 1919, 235 ft. alt., *Luedinghaus* (M); north of Corvallis, 240 ft. alt., July 1920, *Steward 173* (OAC); Salem, 22 July 1920, *M. S. Clemens* (CAS, US); Bush's pasture, Salem, 19 May 1921, *J. C. Nelson 3651* (ANSP); Goshen, Lane Co., 5 July 1922, *Abrams 8716* (P, S); near Albany, 8 July 1923, *Phelps* (CAS); David's Hill, Forest Grove, Washington Co., 15 April 1926, *J. W. Thompson 582* (M); meadows on the Lorane Road, 5 or 6 miles from Eugene, 9 June–18 July 1926, *Henderson* (O); near Alsea, Benton Co., 25 July 1929, *Henderson 11356* (O); Salem, *Reynolds 8988* (Wil.).

Although at first confused with *Sidalcea oregana* and *S. malvaeflora* (especially in name), this species may be separated from all others by its usually hirsute pubescence (except when grown in dense shade), by the pinnatifid segments of the leaves (or long narrow divisions of the uppermost ones), the lax inflorescence with its long pedicels, the pale rose or almost white flowers with dark-tipped calyx, and by its distribution being limited to the Willamette Valley, Oregon. The leaves are yellow-green, thin, softly pubescent, or slightly harsh on the lower surface.

This is without doubt the *Sida malvaeflora* of Lindley,[24] not of DC., although the plant illustrated by Lindley is more like the *Sidalcea asplenifolia* form than the true *S. campestris* of Greene. This could be expected since both seem to have been founded on cultivated forms. The plant of Lindley was introduced by David Douglas from the "Multomah" (Multnomah) region of northern Oregon.

Sidalcea asplenifolia Greene is reported[25] as probably introduced in grass seed in the meadows near Seattle where Piper collected and cultivated it. Most of the specimens distributed under *Piper No. 242* were evidently cultivated, according to a note by him on one of the herbarium sheets. These have extremely large leaves with coarsely serrate-pinnatifid segments and a much elongate, more rigidly erect raceme with smaller flowers and less hirsuteness.

Sidalcea sylvestris Nelson, collected in dense shade of wood-

[24] Lindl. in Bot. Reg. **12**: 1036, *pl. 1036*. 1826.

[25] Piper & Beattie, Fl. N. W. Coast, 238. 1915.

lands near Wheatland, Yamhill Co., Oregon, is almost glabrous, and a much-attenuated shade form of the species. The lower leaves are not present, but the uppermost cauline leaves are not unlike those of the type of *S. campestris.*

10. S. virgata Howell, Fl. N. W. Am. 101. 1897; Piper & Beattie, Fl. N. W. Coast, 239. 1915; Gilkey, Spring Fl. N. W. Oregon, 88. 1929.

Perennial from a woody root, softly stellate-pubescent throughout (rarely glabrescent); stems one or several, up to 6 dm. high, mostly simple, decumbent (rarely rooting) at base; leaves orbicular or semi-orbicular, densely stellate-pubescent on the lower surface with more simple appressed hairs on the upper surface; basal leaves orbicular, small, slightly lobed, lobes coarsely dentate; middle cauline leaves more or less deeply palmately cleft into 5–7 oblong, coarsely dentate segments; upper cauline leaves deeply cleft, segments entire; inflorescence 1–several loose virgate racemes; rhachis, bracts, pedicels, and calyx mostly densely stellate-pubescent; bracts subulate or slightly bidentate, long, often equalling the pedicels, slender; calyx-lobes green or purple-tinged, lanceolate, acuminate; petals bright purple, emarginate, large in the perfect flowers; carpels reticulate with fine short meshes.

Distribution: common on dry hillsides in the Willamette Valley, near Silverton, Corvallis, and Eugene, Oregon.

Specimens examined:

Oregon: 1871 (?), *E. Hall 71* in part (G); Oregon Experiment Station, 21 May 1899, *H. Spencer 2* (OAC); Silverton, June 1882, *T. Howell 680* (US probably authentic material); July to May 1896, Oregon Experiment Station (OAC); Marys River, 13 May 1899, *Getty* (OAC); Corvallis, 5 July 1911, *Griffin* (OAC); near Dallas, 12 May 1911, *Peck 6866* (Wil.); near Salem, 31 May 1913, *Peck 6877* (Wil.); near south College Farm, Corvallis, 14 April 1915, *Yates* (OAC); south of Corvallis, 22 May 1916, *Gilbert 874* (OAC); near Silverton, 11 May 1918, *J. C. Nelson 2122* (G); foothills of Cascades, east of Brownsville, 18 June 1918, *Lawrence 1719* (US); Crystal Lake Cemetery, 7 May 1918, *Gilkey 59* (OAC); Skinner's Butte, Eugene, 8 May 1920, *Brad-*

shaw 1496 (S); border of street, Silverton, 14 May 1921, *J. C. Nelson 3640* (ANSP); dry open hillside, Silverton, 14 May 1921, *J. C. Nelson 3612* (ANSP); Corvallis, 24 May 1922, *Epling 5322* (UCLA); Corvallis, May 1922, *Epling 5611* (UCLA).

This species is very closely related to *S. campestris* but distinct because of the shorter stature and stellate tomentum, leaf form, and usually virgate habit. The leaves and pubescence are much like those of *S. asprella*, but the inflorescence is entirely distinct. It is a species suitable for cultivation.

11. S. neo-mexicana Gray in Mem. Am. Acad. N. S. **4**: 23. 1849 (Pl. Fendl. 23. 1849); Walp. Ann. **2**: 151. 1851–52; Hemsl. Biol. Cent.-Am. Bot. **1**: 99. 1879; Gray in Proc. Am. Acad. **22**: 287. 1887; E. G. Baker in Jour. Bot. **29**: 52. 1891 (Synopsis Malveae, 31. 1894); Coulter in Contr. U. S. Nat. Herb. **2**: 37. 1891; Gray, Syn. Fl. N. Am. **1**^{1}: 306. 1897; Nelson in Coulter & Nelson, Man. Bot. Cent. Rocky Mt. 317. 1909. Hubbard in Bailey, Stand. Cyc. Hort. **6**: 3162. 1917; Rydb. Fl. Rocky Mts. 559. 1917, and ed. 2. 559. 1922.

S. malvaeflora Gray in Smiths. Contr. **3**: 16. 1852 (Pl. Wright. **1**: 16. 1852), mainly, excl. syn. *Sida malvaeflora; ibid.* **5**: 20. 1852 (Pl. Wright. **2**: 20. 1852); Walp. Ann. **4**: 309. 1857, as to synonymy *S. neo-mexicana;* Wats. Bot. King Exp. 46. 1871, mainly, excluding large-flowered form and varieties; Porter & Coulter, Syn. Fl. Colo. 15. 1874; Brew. & Wats. Bot. Calif. **1**: 83. 1876, in part; Hemsl. Biol. Cent.-Am. Bot. **1**: 99. 1879; Greene in Bull. Calif. Acad. Sci. **1**: 75. 1885; Coulter, Man. Bot. Rocky Mt. 41. 1885; Greene, Fl. Francis. 105. 1891, as to description and synonymy *S. neo-mexicana.*

S. parviflora Greene var. *Thurberi* Rob. in Gray, Syn. Fl. N. Am. **1**^{1}: 305. 1897.

S. crenulata A. Nels. in Proc. Biol. Soc. Wash. **17**: 93. 1904; Rydb. Fl. Rocky Mts. 559. 1917, and ed. 2. 559. 1922.

S. neo-mexicana Gray var. *Diehlii* Jones, Contr. West. Bot. 12: 4. 1908.

S. confinis Greene, Cyb. Columb. **1**: 35. 1914.

Perennial from a strong woody fusiform root; stems one to several, simple or much branched, erect or slightly decumbent at

base, 1–9.5 dm. high, hirsute or nearly glabrous (Mexican plants with some few-rayed hairs); leaves with somewhat appressed, simple or few-rayed hairs on both surfaces, ciliate; basal leaves orbicular, 1–6 cm. broad, merely crenate or slightly 5–9-lobed, the lobes crenate or coarsely dentate, sinus open; middle cauline leaves deeply 5–9-parted into 3–5-lobed segments; upper cauline leaves parted almost to the base into 3–5 linear entire segments; stipules lanceolate, ciliate; inflorescence a close many-flowered raceme, elongating after anthesis; rhachis glabrous, or with few simple or few-rayed hairs; bracts 0.5–1 cm. long, deeply bifid or trifid, appearing membranous (whitish opaque or bluish green in color, especially before anthesis), ciliate; pedicels and calyx more or less hirsute, rarely with some stellate hairs (Mexican plants); pedicels strict, after anthesis much longer than the calyx; calyx-lobes deltoid-ovate, acute or acuminate; petals purple, rarely white, about 1.5 cm. long; carpels glabrescent, smooth or slightly reticulate.

Distribution: in moist meadows in the mountains from Wyoming and Idaho south to the states of Coahuila and Durango, Mexico.

Specimens examined:

Wyoming: Cummins, 28 July 1895, *A. Nelson 1463* (CAS, G, M, US); Indian Grove Mts., 17 July 1898, *E. Nelson 4892* (P); Elk Mt., 16 July 1899, *Little & Stanton* (*Pammel 168*) (M); Encampment, Carbon Co., 10 July 1901, *Tweedy 4570* (US); Slater, Carbon Co., 31 July 1903, *Goodding 1747* (C, G, M, US); Jelm, Albany Co., 8 Aug. 1907, *A. Nelson 9069* (G, M).

Colorado: Middle Park, Aug. 1862, *Parry 430* (G, M, US); Rocky Mts., 1862, *Hall & Harbour 18* (F, G); Rocky Mts., 1864, *Parry* (ANSP, US); Musca Pass, Aug. 1867, *Parry 24* (G); North Park, Aug. 1868, *Hayden* (US); South Park, Aug. 1871, *Meehan* (ANSP); Valley of the Upper Arkansas, Trout Creek, Sept. 1873, *Wolf & Rothrock 14* (ANSP, F, US); Grape Creek, 23 June 1873, *T. S. Brandegee 793* (ANSP, C, M); Pleasant Valley, 23 Sept. 1878, *M. E. Jones* (P, S); Middle Park, 2 Aug. 1881, *G. Engelmann* (M); Wagon Wheel Gap, 16 July 1882, *B. H. Smith* (ANSP); Gunnison, July 1888, *Eastwood 13* (US); Table Rock, 7500 ft. alt., 19 July 1891, *Breninger* (M); Steamboat Springs, Sept. 1891,

Trelease (M); Steamboat Springs, July 1891, *Eastwood* (F, G); Hotchkiss, Delta Co., 5200 ft. alt., 23 June 1892, *Cowen 82* (US); Buena Vista, 8000 ft. alt., 5 July 1892, *Sheldon 367* (US); Middle Park, 25 July 1892, *Beardslee 102* (US); Middle Park, Aug. 1892, *Beardslee* (W); North Park, 9000 ft. alt., 9 July 1894, *Crandall 108* (G, SCW); La Veta, 14 July 1896, *Shear 3551* (US); North Park, 19 July 1896, *C. F. Baker* (C); on Grizzly Creek, 8000 ft. alt., 19 July 1896, *C. F. Baker* (M); Durango, 7000 ft. alt., 25 July 1896, *Tweedy 554* (US); Sargent, 27 July 1896, *Shear 5136* (US); Conejos River near Antonito, 7880 ft. alt., 24 June 1898, *Crandall* (US); Durango, 26 July 1898, *Baker, Earle & Tracy 887* (P); Piedra, 12 July 1899, *C. F. Baker 461* (F, G, M, ND, P, US); Ruxton Park, Pike's Peak Trail, Aug. 1900, *Harper & Harper* (M); Gunnison, 7680 ft. alt., 7 July 1901, *C. F. Baker 360* (C, G, M, P, US); Cimarron, 6900 ft. alt., 13 July 1901, *C. F. Baker 440* (C, G, M, ND, P, US); North Elk Canyon, Rio Blanco Co., 12 Aug. 1902, *Sturgis* (CAS, G, S); Steamboat Springs, Routt Co., 20 July 1903, *Goodding 1627* (ANSP, C, G, M, S, US); 10 miles east of Bayfield, 12 Aug. 1904, *Wooton 2671* (US); Mt. Whiteley, 16 July 1905, *Cary 12* (US); Gunnison, 1910, *Evermann* (US); Wagon Wheel Gap, 8400 ft. alt., 15 July 1911, *Murdoch 4756* (F, M, OAC, P); Ortiz, 2400 m. alt., 12 July 1910, *Eggleston 5943* (US); Iron Springs Mesa, San Miguel Co., 7500 ft. alt., 21 Aug. 1912, *E. P. Walker 515* (G, M, P, US); Pitkins, 9200 ft. alt., 12 Sept. 1917, *Clokey 2995* (CAS, F); east of Gunnison, 29 June 1927, *Osterhout* (P).

New Mexico: 1847, *Fendler 79* (ANSP, F, G type, M, US); from western Texas to El Paso, May–Oct. 1849, *Wright 39* (G); Las Playas, June 1851, *Thurber 334, 340* (G type of *S. parviflora* var. *Thurberi* Rob., M); Ojo de Gavilan, Aug. 1851, *Thurber 1664* (G); Rio Laguna, 26 Aug. 1851, *Woodhouse* (ANSP); along the Mimbres, Aug.–Sept. 1851, *Wright 880* (ANSP, C, G, M, US); Ford of Chama, 29 July 1859, *Newberry* (US); Las Vegas, July 1881, *Vasey* (US); Mangas Springs, 15 Oct. 1881, *Rusby 47* (F, G, US); mts. west of Grant's Station, 2 Aug. 1892, *Wooton* (US); Monument No. 40, Mex. boundary line, 15 May 1892, *Mearns 265* (US); Mesquite Spring (Mexico?), 16 May 1892, *Mearns 72* (US type of *S. confinis* Greene, S); Fort Bayard, 25 July 1895,

Mulford 436 (M); Roger's Ranch, 25 July 1895, *Mulford 436a* (M); Mr. Hick's Ranch, 20 July 1895, *Mulford 360* (M); Comanche Valley, 8000 ft. alt., July 1896, *Mrs. H. St. John* (G); along Tularosa Creek, Otero Co., 29 July 1897, *Wooton* (US); White Mountains, Lincoln Co., 5400 ft. alt., 22 July 1897, *Wooton 192* (C, G, M, ND, P, S, US); Chama, 18 July 1898, *Earle* (M); Silver Springs Cañon, Otero Co., 6 July 1899, *Wooton* (M, US); Middle Fork of the Gila, Mogollon Mountains, Socorro Co., 5 Aug. 1900, *Wooton* (US); West Fork of the Gila, Mogollon Mountains, Socorro Co., 6 Aug. 1900, *Wooton* (US); Crain's Ranch, 14 July 1900, *Wooton* (US); Mogollon Mountains, on or near the west fork of the Gila River, Socorro Co., 7500 ft. alt., 4 Aug. 1903, *Metcalfe 366* (G, M, P, US); near Chama, 15 Aug. 1904, *Wooton* (US); Kingston, Sierra Co., 6600 ft. alt., 9 July 1904, *Metcalfe 1091* (M, US); Fort Bayard Watershed, Grant Co., 22 Oct. 1905, *Blumer 119* (G, US); Wheeler's Ranch, 11 July 1906, *Wooton* (C, P, S, US); Pecos River National Forest, 6700 ft. alt., 15 Aug. 1908, *Standley 4966* (G, M, US); along the river, vicinity of Chama, Rio Arriba Co., alt. 2380–2850 m., 8 July 1911, *Standley 6587* (US); Jicarilla Apache Reservation, near Dulce, 2150–2470 m. alt., 20 Aug. 1911, *Standley 8242* (US); Balsam Park, Sandia Mountains, 8200 ft. alt., July–Aug. 1914, *Ellis 244* (M, US); vicinity of Brazos Canyon, Rio Arriba Co., 1 Sept. 1914, *Standley & Bollman 11040* (US); vicinity of Ute Park, Colfax Co., 2200–2900 m. alt., 27 Aug. 1916, *Standley 13872* (US); Las Vegas, San Miguel 7 miles n., 2050 m. alt., 19 July 1927, *Arsène 18632* (P); Las Vegas 6 miles sud., 1880 m. alt., 28 June 1927, *Arsène 18879* (P).

Arizona: Fort Whipple, 1864, *Coues & Palmer* (M); Skull Valley, 4 June 1865, *Coues & Palmer 221* (M); without locality, 1869, *Palmer* (US); moist cañon, 21 July 1896, *Fernow* (US); Huachuca Mts., Sept. 1882, *Lemmon 2646* (C, G); base San Francisco Mts., Aug. 1884, *Lemmon & Lemmon* (C, US); Flagstaff, 5 Aug. 1884, *M. E. Jones 3993* (C, F, P, US); near Flagstaff, 13 July 1889, *Greene* (ND); Johnson, 20 June 1890, *M. E. Jones* (P); Mormon Lake, 10–20 July 1892, *Toumey 80* (C, S, US); San Francisco Mts., 15 July 1892, *Wooton* (US); Prescott, 4 Aug. 1896, *Zuck* (US); vicinity of Flagstaff, 7000 ft. alt., 8 July

1898, *MacDougal 248* (ANSP, C, F, G, US); near Leroux Spring, San Francisco Mts., Forest Reserve, 2200 m. alt., 12 Aug. 1901, *Leiberg 5843* (US); White Mts., 11–15 Aug. 1903, *Griffiths 5259* (M); Coconino National Forest and vicinity, 7250 ft. alt., 8 Sept. 1909, *Pearson 279* (US); Thompson's Ranch, Black River, White Mts., 11 July 1910, *Goodding 527* (G, US); Thompson's Ranch, Black River, 13 July 1910, *Goodding 570* (G); Flagstaff, 7–11 Aug. 1915, *A. E. Hitchcock* (US); Williams, 22 June 1916, *Eastwood 5919* (CAS, G); 3 miles east of Cooley's Ranch, Apache Indian Reservation, 6 July 1918, *Ferris 1279* (S); Riverside Ranger Station, Greer, Apache Forest, Apache Co., 2700 m. alt., 23 Aug. 1920, *Eggleston 17095* (M); valley near Flagstaff, 7000 ft. alt., 28 July 1922, *Hanson 241* (F, M, OAC, P); mountains near Phoenix, 1926, *Norville* (M); about 20 miles south of Prescott, 8 July 1926, *Peebles, Harrison & Kearney 2610* (US); Prescott, 1 June 1927, *Peebles & Harrison 4192* (US); near Prescott, 17 July 1927, *Peebles, Harrison & Kearney 4314* (US); Ryan Ranch, Apache Reservation, 2 Oct. 1927, *Harrison 4861* (C, US).

IDAHO: American Falls, Oneida Co., 3000 ft. alt., 28 July 1911, *Nelson & Macbride 1386* (C, G, M, P, RM, S, US).

UTAH: *Fremont's 2nd Expedition* (US); southern Utah, 1874, *Parry* (M); 1877, *Palmer 61* (M); Springville, 26 June 1880, *M. E. Jones* (P); Salt Lake City, 23 June 1883, *Leonard* (G); Deep Creek, 28 July 1891, *M. E. Jones* (P); Fairview, 6000 ft. alt., 13 June 1894, *M. E. Jones 5627a* (P, US); Marysvale, 6500 ft. alt., 1 Aug. 1894, *M. E. Jones 5976b* (P, US); Kingston, 6500 ft. alt., 3 Sept. 1894, *M. E. Jones 5983a* (P, US); Juab, 10 June 1902, *Goodding 1091* (C, F, G, M, P, RM TYPE of *S. crenulata* Nels., US); Wasatch Co., near Midway, 6 July 1905, *Carlton & Garrett 6694* (RM, US); Hills Park, 29 June 1908, *Mrs. Joseph Clemens* (ANSP, F, G, M, S); Summit Co., 11 Aug. 1908, *Garrett 2303a* (Gar.); mesa east of Monticello, 2100 m. alt., 25 July 1911, *Rydberg & Garrett 9211* (Gar., US); Montezuma Canyon, east of Monticello, 2000 m. alt., 13 Aug. 1911, *Rydberg & Garrett 9680* (G); Toole Co., 17 June 1914, *Garrett 2762* (G); Parley's Canyon, Salt Lake Co., 29 June 1915, *Garrett 2803a* (Gar.); near Garfield, Salt Lake Co., 16 June 1915, *Garrett 2793* (Gar., RM); Antelope Island, Great Salt Lake, Salt Lake Co., 4250 ft. alt.,

11 June 1916, *Garrett 2820* (Gar.); Murray, Salt Lake Co., 23 July 1917, *W. W. Jones 412* (G); north of Salt Lake City, Salt Lake Co., 12 June 1926, *Garrett 3501c* (RM); Wasatch Co., 8 Aug. 1928, *Garrett* (Gar.).

Nevada: Wells, 5700 ft. alt., 9 Aug. 1881, *M. E. Jones 2182* (C, CAS, P, S); pasture at Simon's Creek, Elko Co., 15 Aug. 1902, *Kennedy 673* (RM); Stampede, Elko Co., Aug. 1903, *Kennedy 811* (RM); Deeth, Elko Co., 5340 ft. alt., 17 July 1908, *A. A. Heller 9016* (ANSP, M, US); Italian Ranch, N. C. Railroad, Reese River Valley, Lander Co., 6000 ft. alt., 22–25 July 1913, *Kennedy 4126* (ANSP, M, US); between Battle Mountain and Austin, 1950 m. alt., 25 July 1913, *A. E. Hitchcock 696* (US); Park's Station, 25 miles north of Elko, 1950 m. alt., 3 Aug. 1913, *A. E. Hitchcock 981* (US); Duck Creek, Paine's Ranch, Ely, 17 Aug. 1913, *A. E. Hitchcock 1356½* (US).

Mexico:

Chihuahua: fifteen miles south of Guadalupe y Calvo, 7500–8000 ft. alt., Aug. 1898, *E. W. Nelson 4823* (US); Sierra Madre, near Guachochi, 27 Sept. 1898, *Goldman 176* (G, US); Sierra Madre near Colonia Garcia, 8000 ft. alt., 25 June 1899, *Townsend & Barber 55* (C, F, G, M, US); Sierra Madre, 21 June–29 July 1899, *E. W. Nelson 6044* (US); Round Valley, Sierra Madre Mts., 17 Sept. 1903, *M. E. Jones* (CAS, P type of *S. neo-mexicana* var. *Diehlii* Jones, S, US); vicinity of Madera, 2250 m. alt., 27 May–3 June 1908, *Palmer 310* (US); vicinity of Chihuahua, 1300 m. alt., 8–27 April 1908, *Palmer 64* (F, M, US).

Durango: City of Durango and vicinity, April–Nov. 1896, *Palmer 117* (C, F, G, M, US); near El Salto, 12 July 1898, *E. W. Nelson 4543* (US); *P. Ibana Garcia 321* (US).

Nuevo Leon (?): marsh of San Juan de la Vaqueria, 20 May 1847, *Gregg 718* (G, M).

Coahuila: Buena Vista, near Saltillo, 24 July 1848, *Gregg 291* (G, M); Saltillo and vicinity, May 1898, *Palmer 132* (C, G, M, US).

This species was formerly confused with *Sidalcea malvaeflora* as to name, and horticultural forms of *S. neo-mexicana* are sold under the name *S. malvaeflora* at present. The geographical distribution clearly indicates this species as having the widest

range of any within the group, reaching Montana on the north, western Texas on the east, and the States of Nuevo Leon and Durango, Mexico, on the south. Dr. Gray made use of this in connection with specific characters in finally separating *S. malvaeflora* into the coastal species retaining the name *S. malvaeflora*, and the two inland species *S. neo-mexicana* with the range just given, and *S. oregana* for the more northern forms ("West side of the Rocky Mountains," *Nuttall*).

Sidalcea parviflora var. *Thurberi* Rob.[26] (locality given as Las Playas, Sonora, Mexico), doubtless from Las Playas,[27] New Mexico, near the United States-Mexican border, is a low, small-leaved form found in alkaline soil and yet not sufficiently unlike other small forms to be given varietal rank. Though resembling in some degree the plant designated as *S. parviflora* by Greene, it is more nearly related to *S. neo-mexicana.*

Sidalcea crenulata A. Nelson, from Juab, Utah, *Goodding No. 1091*, has more stellate pubescence in the inflorescence (thus simulating some Mexican forms) than most of the group but otherwise does not differ from typical *S. neo-mexicana.*

Sidalcea neo-mexicana var. *Diehlii* M. E. Jones is typical of the taller Mexican forms, most of which have a greater degree of hirsute pubescence, and larger, more conspicuous bracts than the more northern forms. The collection of *Townsend & Barber No. 55*, from Chihuahua, shows this character in striking contrast to *Palmer No. 64*, from Chihuahua, which is smaller, less hirsute or merely stellate-pubescent, and with lighter-colored flowers.

Sidalcea confinis Greene was based on a very much reduced plant from Mesquite Spring,[28] Mexico (near Monument 46, now New Mexico), 16 May 1892, *Mearns No. 72*. One other specimen collected near Monument no. 40[28] (Mexican Boundary line), 15 May 1892, *Mearns No. 265*, is identical. Monument no. 40 is just south of the Big Hatchet Mountains, New Mexico, and these plants from alkaline soils resemble those from Las Playas not far distant. Due to the alkalinity of that area they are much

[26] Robinson in Gray, Syn. Fl. N. Am. **1**[1]: 305. 1897.

[27] Wooton in Bull. Torr. Bot. Club **33**: 561–566. 1906; Standley in Contr. U. S. Nat. Herb. **13**: 143. 1910.

[28] Rept. U. S. & Mex. Bound. Com. (Sen. Doc. 247) **2**: 17. 1898.

reduced, whitish, less hirsute, and have much smaller bracts than the montane forms.

11a. Var. **parviflora** (Greene) Roush, n. comb.

S. parviflora Greene in Erythea **1**: 148. 1893; Gray, Syn. Fl. N. Am. **1**[1]: 305. 1897; Abrams, Fl. Los Angeles & Vicinity, 248. 1904; Davidson & Moxley, Fl. So. Calif. 231. 1923; Jepson, Man. Fl. Pl. Calif. 631. 1925.

S. nitrophila Parish in Erythea **7**: 93. 1899; Davidson & Moxley, Fl. So. Calif. 231. 1923.

More or less glabrous and glaucous throughout; stems several, slender; leaves thick, with few, simple, geminate, or few-rayed hairs on the veins of the lower surface, sparse on the upper surface; inflorescence racemose, elongating in anthesis; bracts less conspicuous than in the species; pedicels and calyx somewhat stellate-pubescent; carpels dorso-laterally reticulate.

Distribution: in brackish and subalkaline marshes of Kern, San Bernardino, Orange, and Los Angeles Counties, California.

Specimens examined:

California: san bernardino county—San Bernardino, April 1885, *Parish & Parish 1747* (G); San Bernardino, May 1886, *Parish & Parish 1747* (US); Rabbit Springs, Mohave Desert, May 1886, *S. B. Parish 1804* (G, ND cotype of *S. nitrophila* Parish, S); meadows, 15 May 1889, *S. B. Parish 2080* (G type, M, ND); alkaline soil, ——— Ranch, May 1891, *S. B. Parish* (S); meadows, San Bernardino, May 1891, *S. B. Parish* (P); meadows near San Bernardino, 10 June 1891, *S. B. Parish 2199* (ND, US); vicinity of San Bernardino, 1000–1500 ft. alt., 1 May 1895, *S. B. Parish 3639* (C, CAS, G, M, ND, SCW, US); San Bernardino, 30 April 1896, *Cummings* (G); vicinity of San Bernardino, 1000–2500 ft. alt., April 1899, *S. B. Parish* (P); vicinity of San Bernardino, 1000 ft. alt., 22 April 1901, *S. B. Parish 4687* (S); Rabbit Springs, Mohave Desert, 1 June 1901, *S. B. Parish 4854* (ANSP, C, P, S, US); Chino, 700 ft. alt., 26 April 1902, *Kellogg* (P); Chino Creek, south of Ontario, 500 ft. alt., 30 May 1917, *Johnston 1127* (P, S, US); Rabbit Springs, 24 April 1915, *S. B. Parish 9823* (C, S); Twenty-nine Palms, 3000 ft. alt., 1 May 1921, *Munz 4516* (P); San Bernardino Mts.,

June 1928, *Van Dyke* (CAS); LOS ANGELES COUNTY—Antelope Valley, 1884, *Oliver* (G); Elizabeth Lake, June 1887, *S. B. Parish 1956* (ND, S); Santa Monica, 1890, *Hasse* (C); near Santa Monica, 1891, *Hasse* (C, ND, US); Santa Monica, June 1892, *Hasse* (C); Claremont, 12 June 1909, *Pruett 67* (P); ORANGE COUNTY—between Tustin and Myford, 17 April 1903, *Abrams 3257 & 3257a* (ANSP, C, G, M, ND, P, S, US); KERN COUNTY—Posa Creek, Sept. 1853, *Heermann* (US); Fort Tejon and vicinity, 1857–8, *Vesey 15* in part (US); near Rosamond, 15 May 1896, *Davy 2255* (G); near Fort Tejon, 26 May 1896, *Davy 2336* (C); Costac Lake, Tejon Pass, 12 June 1896, *Dudley & Lamb 4450* (P, S, US).

Dr. Greene referred this group to *Sidalcea neo-mexicana* until he found "*S. glaucescens*" written on the sheets from Parish's herbarium. He then described it as *S. parviflora* and related it to the inland species *S. malvaeflora* (now *S. neo-mexicana*). The habit, with leaves mostly basal, sparse hirsute hairs, elongate inflorescence, long pedicels, and membranous bracts, warrants maintaining it as a variety of the inland species, connecting that species with the *S. malvaeflora* of the coast. The subalkaline or subsaline (brackish) habitat may account for the reduced leaf surface, the sparse pubescence, and the smaller bracts. Forms cultivated from the seed of plants collected by Hasse in the Los Angeles vicinity resemble closely the Rocky Mountain forms of the species, especially *Rusby No. 47* from Mangas Springs, New Mexico.

11b. Var. **Covillei** (Greene) Roush, n. comb.

S. Covillei Greene, in Cyb. Columb. **1**: 35. 1914.

Sparsely stellate-pubescent throughout; stems erect, several; leaves mostly basal, slightly to deeply cleft into short, obovate, crenate or dentate lobes; inflorescence an elongate raceme; bracts not conspicuous; carpels reticulate with short meshes.

Distribution: western part of Inyo County, California.

Specimens examined:

CALIFORNIA: INYO COUNTY—about 1 mile north of Lone Pine, 1125 m. alt., 14 June 1891, *Coville & Funston 954* (US); Hawee meadows, 20 June 1891, *Coville & Funston 1004* (US TYPE);

Lone Pine, 6000 ft. alt., 14 May 1897, *M. E. Jones* (M, P, S, US); near Bishop, 17 June 1927, *M. E. Jones* (CP, P).

This variety differs from var. *parviflora* chiefly in the presence of stellate hairs which may be a response to its habitat in this arid region.

12. **S. malvaeflora** (DC.) Gray in Benth. Pl. Hartw. 300. 1848; in Smiths. Contr. **3**: 16. 1852 (Pl. Wright. **1**: 16. 1852), at least as to name carrying synonymy; Wats. Bot. King Exp. 46. 1871, as to name and synonymy only; Brew. & Wats. Bot. Calif. **1**: 83. 1876, as to synonym *Sida malvaeflora* DC.; Gray in Proc. Am. Acad. **21**: 409. 1886; *ibid.* **22**: 286. 1887, not of earlier publications except as to synonym *Sida malvaeflora* DC.; Greene, Fl. Francis. 105. 1891, in part; E. G. Baker in Jour. Bot. **29**: 52. 1891 (Synopsis Malveae, 30. 1894); Gray, Syn. Fl. N. Am. **1**^{1}: 304. 1897; Howell, Fl. N. W. Am. 101. 1897, name only; Jepson, Fl. West. Mid. Calif. 239. 1901, in part, and ed. 2. 258. 1911; Abrams, Fl. Los Angeles & Vicinity, 247. 1904; Hubbard in Bailey, Stand. Cyc. Hort. **6**: 3162. 1917, name only; Jepson, Man. Fl. Pl. Calif. 628. 1925.

Pl. 5, figs. 1 & 2; pl. 11.

Sida malvaeflora DC. Prod. **1**: 474. 1824 (Mocino & Sesse, Fl. Mex. Ic. ined., and Calques des Dess. *pl. 70*, doubtless collected at Monterey, California); Torr. & Gray, Fl. N. Am. **1**: 234. 1838, and Suppl. 681. 1840, as to coastal spp. only; Hook. Fl. Bor.-Am. **1**: 108. 1840, in part, as to coastal spp. only; Hook. & Arn. Bot. Beech. Voy. Suppl. 326. 1840, as to name only.

Nuttallia malvaeflora Fisch. & Trautv. in Fisch. & Mey. Ind. Sem. Hort. Petrop. **3**: 41. 1837.

Sida delphinifolia Nutt. in Torr. & Gray, Fl. N. Am. **1**: 235. 1838; Walp. Rep. **1**: 316. 1842.

Sidalcea humilis Gray in Mem. Am. Acad. N. S. **4**: 20. 1849 (Pl. Fendl. 20. 1849); Walp. Ann. **2**: 151. 1851–52; Brew. & Wats. Bot. Calif. **1**: 84. 1876; Greene in Bull. Calif. Acad. Sci. **1**: 75. 1885; Gray in Proc. Am. Acad. **21**: 409. 1886.

S. delphinifolia (Nutt.) Greene, Fl. Francis. 105. 1891, not of Gray, Pl. Fendl.

S. delphinifolia (Nutt.) Greene var. *humilis* Greene, Fl. Francis. 106. 1891.

S. scabra Greene in Pittonia **3**: 158. 1897.

S. rostrata Eastwood in Bull. Torr. Bot. Club **29**: 80. 1902.

Perennial from a woody root, glabrescent, retrorsely hirsute (especially below), or with some stellate pubescence; stems several, simple or branched, partially decumbent to suberect, 0.5–8.5 dm. high; basal leaves orbicular, 1–8 cm. broad, crenate, or laciniately toothed, or slightly lobed, the lobes cuneate-obovate and variously dentate, the upper surface with appressed hairs, the lower surface with sparse stellate pubescence mixed with hirsute pubescence; cauline leaves more or less lobed or parted into linear or narrowly oblong, rather coarsely dentate segments, pubescence as for the basal leaves; stipules green or purplish, lanceolate or ovate and ciliate (if subulate, pubescent throughout); inflorescence a loose raceme, flowers large and often one in the axil of some of the uppermost leaves; bracts ovate, bidentate or deeply bifid, the lobes lanceolate or subulate, merely ciliate or pubescent; calyx more or less stellate-pubescent with some long hirsute hairs; the lobes often nerved, ovate-deltoid, becoming deltoid-lanceolate or lanceolate; petals purple or rose-purple (rarely white), emarginate, up to 2.5 cm. long; anthers rarely purple; young carpels glabrous (rarely hirsute), mature carpels favose-reticulate on sides and back.

Distribution: along the coast from southern Oregon to northern Lower California, Mexico.

Specimens examined:

Oregon: Gold Beach, 1 June 1915, *Hoyt 71* (S); Port Orford, 20 June 1919, *Peck 9068* (G, M); Port Orford, 15 June 1926, *Peck 14669* (Wil.).

California: humboldt county—Bucksport, 11 June 1905, 0–500 ft. alt., *Tracy 2193, 2194* (C); near Hydesville, 100–300 ft. alt., 11 May 1912, *Tracy & Babcock 3595* (C); near Hydesville, 100–300 ft. alt., 11 May 1912, *Tracy & Babcock 3596* (C); near Hydesville, 100–300 ft. alt., 11 May 1912, *Tracy & Babcock 3597* (C); Alton, 100–300 ft. alt., 9 June 1912, *Tracy 3669* (C, US); Kneeland Prairie, 2500 ft. alt., 28 June 1925, *Kildale 803* (S); Alton Hill, 100 ft. alt., 23 March 1926, *Kildale 1603* (S);

Gans Prairie, 2000 ft. alt., 10 July 1927, *Kildale 3727* (S); MENDOCINO COUNTY—near Ukiah, 1897, *Purdy* (C); near Mendocino, from sea-level to 500 ft. alt., June 1898, *H. E. Brown 815* (C, M, US, COTYPES of *S. rostrata* Eastwood); Fort Bragg, 8–16 Aug. 1912, *Eastwood 1608* (CAS); Fort Bragg, 6 July 1920, *Duncan 155* (S); Mendocino City, 28 June 1922, *Eastwood 11465* (CAS, US); SONOMA COUNTY—*Samuels 31* (US); near Healdsburg, April 1897, *King* (C); beach from Sea View to Stewart's Point, 5 April 1897, *M. S. Baker* (C); Dillon's Beach, April 1899, *M. S. Baker* (P); three miles south of Healdsburg, 9 April 1902, *Heller & Brown 5235* (ANSP, F, G, M, P, S, US); Bennett Valley, southeast of Santa Rosa, 8 April 1902, *Heller & Brown 5227* (S, US); Petaluma, 7 March 1913, *Condit* (C); road to Bodega Point, 13 May 1917, *Eastwood* (CAS); near Healdsburg, 27 April 1918, *Abrams 6921* (S); Petaluma, 8 May 1921, *Eastwood 10460* (CAS); Petaluma, 24 April 1924, *M. E. Jones* (P); MARIN COUNTY—Angel Island, 14 March 1876, *McLean* (C); Liberty's, 1 May 1890, *K. Brandegee* (C); San Rafael, 6 May 1893, *Blankinship* (G); near Tiburon, April 1895, *Sonne 1428* (C); on the Fairfax Road, 18 April 1897, *Eastwood* (US); Bodega Bay, 25 May 1900, *Chandler 713* (C); Mt. Tamalpais, 26 Feb. 1900, *Chandler 529* (C); Pt. Reyes, May 1906, *Eastwood* (CAS); Kentfield, 30 April 1912, *Parsons* (CAS); Kentfield, 19 May 1912, *Eastwood 25* (CAS, G, M, US); Sausalito, 6 March 1913, *Schmitt* (US); Tocaloma, 4 April 1917, *Mason 79* (S); near Pt. Reyes station, 13 May 1917, *Eastwood* (CAS); Lagunitas, 28 April 1918, *Grinnell* (S); Kentfield, 27 March 1921, *Epling 5197* (M); Sausalito, 1 April 1921, *Eastwood* (CAS); Pt. Reyes, 13 May 1923, *Eastwood 11807* (CAS); Mill Valley, 30 March 1929, *Raven* (CP); NAPA COUNTY—Napa Valley, 5 May 1853–4, *Bigelow* (G, US); Vineland, 26 April 1893, *Jepson* (C, US); Napa, 24 April 1924, *M. E. Jones* (CAS, P); SOLANO COUNTY—Chandler's Field, Arequipa Hills, 2–6 May 1891, *Jepson* (C, US); Vallejo, 15 April 1914, *W. W. Jones 131* (G); CONTRA COSTA COUNTY—Byron, 1892, *Bioletti* (ND TYPE of *S. scabra* Greene); Camp 69, Walnut Creek, 30 April 1862, *Brewer 1002* (G, US, C); Moraga Valley, 31 March 1917, *Evermann* (CAS); ALAMEDA COUNTY—Oakland, 1863, *Holder 2537* (US); Mission, Oakland, March 1867, *Rattan* (S);

Oakland, 18 March 1888, *Drew* (C); Alameda, 11 May 1891, *Greene* (C, US); near Newark, 6 May 1895, *Davy 1101* (C, ND); Berkeley, 22 Feb. 1899, *Chandler 214* (C); north Berkeley, April 1899, *H. M. Hall* (G); Berkeley Hills, 7 May 1901, *Chandler 1020* (US); hills near Berkeley, 1000 ft. alt., 12 April 1902, *Tracy 1363* (C, P); Berkeley Hills, 26 April 1903, *Mulliken 35* (C); Berkeley, May 1906, *Eastwood* (CAS); vicinity of Berkeley, May–June 1906, *Walker 83* (C); Thousand Oaks, near Berkeley, 28 March 1920, *Johnston* (P); Claremont Cañon, back of Berkeley, 3 April 1920, *Johnston* (P); SAN FRANCISCO COUNTY—*Williamson* (ANSP); San Francisco, 1865, *Bolander 12* (G, M); San Francisco, 8 March 1868, *Kellogg & Harford 108* (CAS, M, US); Mission Dolores, San Francisco, 188–, *Kellogg* (S); Presidio, 28 May 1887, *B. H. Smith* (ANSP); near San Francisco, 1888, *Greene* (CAS); San Francisco, May 1891, *T. S. Brandegee* (C); Lake Merced, May 1893, *Michener & Bioletti* (*1344a* ?) (C, M, US, W); San Francisco, June 1893, *T. S. Brandegee* (C); San Francisco, April 1894, *Eastwood* (G); between Ocean View and Lake Merced, 24 March 1895, *Dudley* (S); San Francisco, 19 Jan. 1895, *Cannon* (G); San Francisco, 10 April 1897, *Blasdale* (C); San Francisco, 23 April 1907, *K. Brandegee* (C, P); Lake Merced, San Francisco, 23 April 1907, *K. Brandegee* (C); near San Francisco, 20 March 1913, *Schmitt* (US); SAN MATEO COUNTY—Pescadero Ranch, 25 May 1861, *Brewer 667* (C, M, US); mountains back of San Mateo, 11 June 1887, *Greene* (ANSP, C); 22 March 1894, *Tidestrom* (C); near Pebble Beach, Pescadero, 25 March 1894, *Dudley* (S); woodside to Crystal Springs, May 1894, *Dudley* (S); Millbrae, 20 April 1895, *Davy 1024* (C); Pebble Beach Pasture, Pescadero, 19 April 1896, *Dudley* (S); by road, top of Montara Mts., 17 May 1900, *Dudley* (S); Colma, 5 May 1901, *Abrams 1602* (S); San Bruno Hills, May 1903, *Elmer 4637* (C, CAS, M, OAC, P, S, US); near Adelanta Villa, March 1903, *Davis* (S); Cahil Ridge below McFarland's, 10 June 1906, *Dudley* (S); Crystal Springs, 10 June 1902, *Eastwood 329* (CAS, US); Crystal Springs, 1912, *Eastwood* (CAS); n. pt. of Half Moon Bay, 10 March 1916, *Stinchfield 268* (S); Moss Beach, 18 March 1917, *Browne* (W); Lagoon of Arroyo de los Frijoles, 100 ft. alt., 26 April 1920, *Ferris 1972* (S); Rockaway Beach,

summer 1925, *Kelley* (CAS); SANTA CLARA COUNTY—Alma, 24 May 1889, *Hasse* (M); between Lake Lagunita and Adelanta Villa, Stanford University, 3 May 1893, *Dudley* (S); Evergreen, 11 April 1893, *Davy 51* (C); Stanford University, April 1898, *Abrams* (S); near Evergreen, east of San Jose, 7 May 1898, *Dudley* (S); Stanford University, Feb. 1900, *Atkinson* (S); Stock-farm hills, 22 Feb. 1900, *Wight 102* (US); Stanford University, March 1901, *Abrams 1128* (M, P); Stanford University, 5 April 1902, *Abrams 2302* (G, M, S, US); near Stanford University, 9 March 1902, *C. F. Baker 275* (C, G, M, P, SCW, US); near Stanford University, 15 April 1902, *C. F. Baker 611* (C, CAS, F, G, M, ND, P, S, US); Stanford University, 15 April 1902, *C. F. Baker* (P); Palo Alto, 19 April 1910, *Mrs. T. C. Pease* (G); Canada Valley, near Gilroy, 3 April 1915, *J. W. Sheldon* (S); SANTA CRUZ COUNTY—Coast Region, 17 May 1902, *C. H. Thompson* (S); Santa Cruz, 19 April 1904, *Berg* (C); near Glenwood, 800–900 ft. alt., 17 June 1909, *R. J. Smith 11* (ANSP, C); Swanton, 12 May 1912, *Rich* (S); Santa Cruz Island, 6 June 1918, *Miller* (CAS); SAN BENITO COUNTY—Hollister, 14 April 1897, *Setchell* (C); MONTEREY COUNTY—Soledad, 20 April 1882, *M. E. Jones 3157* (CAS, M, P, US); 1883, *Meehan* (ANSP); Monterey, June 1889, *K. Brandegee* (C); March–May 1889, *Abbott* (CAS, G); Pacific Grove, Monterey, 25 March 1895, *Rutter 123* (US); Pacific Grove, 24 May 1899, *Chandler 318* (C); east of Carmel-Salinas divide, 10 June 1901, *Dudley* (S); Pacific Grove, April 1902, *Elmer 3569* (C, CAS, G, M, S, US); along railroad near Seaside, beyond Del Monte, 13 April 1903, *A. A. Heller 6567* (ANSP, C, G, M, P, S, US); Rancho Encinal, 13 April 1903, *Kellogg* (G); Monterey, June 1903, *A. A. Heller* (US); Pacific Grove, along the beach, 7 May 1903, *A. A. Heller* (G); Pacific Grove, 22 May 1903, *A. A. Heller* (G, M); forest near Carmel Bay, 5 July 1905, *Coleman* (S); Carmel Valley, 1 mile above the Mission, 2 April 1907, *Abrams 6424* (S); Pacific Grove, 12 June 1907, *Patterson & Wiltz* (CP); 17-mile Drive near Pebble Beach, 4 April 1909, *Abrams 4225* (S); dunes, Carmel, 7–10 Jan. 1910, *Mrs. T. C. Pease* (G); Carmel-by-the-Sea, 8 Feb. 1910, *Randall 13* (S); back of Pebble Beach Lodge, 17-mile Drive, 28 March 1910, *Randall 156* (S); near burnt district, 17-mile Drive, 30

March 1910, *Randall 196* (S); Carmel-by-the-Sea, 10 April 1910, *Randall 303* (S); Carmel-by-the-Sea, 10 April 1910, *Randall* (P); near Pebble Beach, 17-mile Drive, 30 April 1910, *Randall 430* (S); Cypress Pt., 28 May 1912, *Eastwood 82* (CAS, US); Pt. Pinos, 9 March 1913, *Eastwood 2492* (CAS); Pacific Grove, 8 July 1914, *Newell* (CAS); San Juan Grade, 2 April 1917, *Abrams 6429* (S); Carmel Highlands, 1 Jan. 1925, *Epling 6224* (M, UCLA); Carmel Highlands, 1 Jan. 1925, *Epling 6292* (M, UCLA); SAN LUIS OBISPO COUNTY—wooded hills, *Summers* (C); San Luis Mts., 19 April 1882, *Summers* (C); San Luis Valley, 17 March 1886, *Summers* (C); San Luis Mts., 27 April 1886, *Summers 102* (C); San Luis Mts., 23 Nov. 1888, *Summers* (C); Arroyo Grande, May 1895, *King* (C); 1 mile south of Santa Margarita, 14 April 1925, *Bacigalupi 1152* (S); 3 miles west of San Luis Obispo, 24 March 1925, *Munz 9233* (C, P); Avila, 3 May 1926, *Eastwood 13798* (CAS); roadside 3 miles east of Templeton, *Wiggins 2075* (S); Morro, *Eastwood 14310* (CAS); Morro, *Barber* (C); SANTA BARBARA COUNTY—*Nuttall* (ANSP TYPE of *Sida delphinifolia* Nutt., G); *Gibbons 117* (ANSP); 1845–7, *Fremont's Expedition to California* (ANSP); Santa Barbara, near the sea, on foothills, March 1861, *Brewer 280* (G, US); Santa Barbara, July 1875, *Rothrock 14* (G); Point Salinas, May 1893, *Blockman* (C); 20 March 1896, *Hubby 67* (C); Cuyama, Caliente Creek, 6 May 1896, *Eastwood* (C); Casmalia, 13 June–3 July 1906, *Eastwood 830* (CAS); Lompoc, 30 April 1926, *Eastwood 13717* (CAS); VENTURA COUNTY—Ojai, 10 April 1866, *Peckham* (US); Goodenough Meadow, 28 June 1896, *Dudley & Lamb 4728* (P, S); Ojai Valley, 5, 8 May 1896, *Hubby 28* (C, G); Ojai Valley, 8 May 1902, *H. M. Hall 3196* (C); Upper Sonoran Zone, 5 July 1905, *H. M. Hall 6503* (C); Seymour Creek, Mt. Pinos, 5900 ft. alt., 10 June 1923, *Munz 6975* (P); Camarilla, 27 April 1926, *M. E. Jones* (P); RIVERSIDE COUNTY—San Jacinto Mts., 23 July 1890, *Orcutt* (M); San Jacinto, 1890, *Gregory* (C); San Jacinto Mts., 6000 ft. alt., 28 July 1897, *H. M. Hall 739* (C, US); Strawberry Valley, 6000 ft. alt., June 1897, *H. M. Hall 674* (C); San Jacinto Mts., 6000 ft. alt., Aug. 1897, *H. M. Hall* (M); Beaumont, 18 April 1897, *H. M. Hall 468* (C); San Jacinto Mts., May 1899, *H. M. Hall* (C); Santa Ana Mts., canyons near

Murietta, 29 March 1916, *Robinson & Crocker* (M, P, US); Corona, 27 April 1918, *Munz 2144* (P); between Banning & Cabazon, 11 April 1920, *Jaeger 186* (US); Idyllwild, San Jacinto Mts., 5300 ft. alt., 1 June 1921, *M. F. Spencer 146* (C, G, P, US); Lamb's Canyon, near Banning, 2200 ft. alt., 25 April 1922, *M. F. Spencer* (M); Lamb's Canyon, near Banning, 2300 ft. alt., 25 April 1922, *M. F. Spencer 2016* (ANSP, G); Hemet Valley, 1 mile above Garner Ranch, 4550 ft. alt., 19 May 1922, *Munz & Johnston 5441* (C, P); Hemet Valley, 4600 ft. alt., 19 May 1922, *Munz & Johnston 5428* (P); San Jacinto Mts., 18 June 1922, *M. F. Spencer* (P); Coahuila Valley, 21 May 1927, *Munz 10836* (P); Idyllwild, 22–28 July 1928, *Van Dyke* (CAS); ORANGE COUNTY—San Juan, 5 April 1923, *Pierce* (P); LOS ANGELES COUNTY—Los Angeles, July 1897, *Nevin* (ANSP); Los Angeles, 188–, *Nevin 254* (ANSP, S); Los Angeles, 24 March 1889, *Fritchey 24* (M); grassy plains, May 1890, *Hasse 22* (US); plains, May 1891, *Hasse* (C, US); 1891, *Davidson* (S); Pomona, 1891, *Bereman 915* (M); 1895, *Davidson* (C); Leonis Valley, 20 May 1896, *Davy 2631* (G); San Dimas, 1500 ft. alt., 14 March 1897, *Chandler* (C); Santa Monica Forestry Station, 21 March 1897, *Barber* (C); Paloma, 1 Aug. 1898, *T. S. Brandegee* (S); Mink Hill, Pasadena, 11 Feb. 1900, *G. B. Grant 2716* (S); 1000 ft. alt., 1 March 1901, *G. B. Grant 3507* (US); Eagle Rock Valley, 17 March 1901, *G. B. Grant 9190* (S); Puete, 2 April 1901, *Shaw 583* (S); Pasadena near Devil's Gate, 8 April 1901, *Abrams 1436* (P, S); Eagle Rock Canyon, 16 March 1902, *Braunton 182* (US); Pasadena, Oak Knoll, 4 May 1904, *G. B. Grant 6172* (S); Pomona, Claremont, 28 March 1915, *Coleman* (P); KERN COUNTY—Tehachapi, 5 May 1905, *A. A. Heller 7830* (ANSP, F, G, M, S, US); Tehachapi, 15 May 1905, *K. Brandegee* (C); Johnson Canyon, Walker Basin, 3 June 1905, *Grinnell 86, 87* (US); Tehachapi, 13 May 1913, *Eastwood 3244* (CAS, G, US); Weldon, 19 April 1915, *Evermann* (CAS, US); Tehachapi Valley, 3950 ft. alt., 23 May 1925, *Feudge 1159* (P); SAN BERNARDINO COUNTY—April 1884–5, *Antisell 30* (G); San Gorgonio Pass, 1881, *Parry* (M); clay foothills, Highlands, 17 April 1889, *S. B. Parish 2067* (F, G, ND, S); Highlands, 15 May 1891, *S. B. Parish 2198* (OAC, SCW, US, W); near Adelanta Valley, 22 April 1894, *Dudley* (S); vicinity of San

Bernardino, 1000–2500 ft. alt., May 1897, *S. B. Parish* (M, S); San Bernardino, 1000–2500 ft. alt., 11 May 1895, *S. B. Parish 3640* (C, CAS, G, US); San Gorgonio Pass, 600 m. alt., 5 April 1898, *Leiberg 3248* (US); Redlands, 4 Feb. 1904, *Berg* (C); Stewart's Pond, 4 May 1904, *Wilder* (P); Sand Canyon, Yucaipa, May 1906, *G. B. Grant 475* (CAS); roadside near Parish Ranch, 19 May 1907, *Reed 1351* (P); San Bernardino Valley, 300 m. alt., 8 June 1908, *S. B. Parish 6957* (C); Sand Canyon, near Redlands, 25 May 1918, *S. B. Parish 11783* (M, P); Holcomb Creek, Santa Ana Tributary, 23 June 1922, *Peirson 2056* (S); Yucaipa, 2750 ft. alt., 10 May 1924, *Feudge 815* (P); below Mill Creek Power Station at Yucaipa Road, 7 July 1927, *Craig, Newsom & Hilend 337* (M, P); SAN DIEGO COUNTY—May 1852, *Thurber 559* (G, US); 1874, *Cleveland* (G, M); Cuiamaca Mts., July 1875, *Palmer 24* (C, F, M); Chollas Valley, 10 April 1884, *Orcutt 305* (F, US); Laguna, 16 April 1889, *Orcutt* (M); at San Diego, 3 April 1891, *Dunn* (S, W); Escondido, March 1893, *King* (C); San Ysabel, 19 April 1893, *Henshaw 121* (US); Encinitas, April 1894, *Angier* (US); 9 May 1894, *T. S. Brandegee* (C); Witch Creek, May 1894, *Alderson* (G, ND, S); Laguna Mts., 20 June 1904, *T. S. Brandegee* (C); Del Mar, 24 March 1895, *Angier 90* (M); San Diego, 5 June 1895, *Stokes* (S); on the mesa, 21 March 1896, *Cummings* (G); San Diego, April 1897, *Wislizenus 915* (M); April 1901, *K. Brandegee* (C); San Diego, 19 March 1901, *Setchell* (C, M); April 1902, *G. B. Grant 2004* (C, S); near Fallbrook, 26 April 1903, *Abrams 3311* (ANSP, G, M, P, S, US); Hill Valley near Campo, 2 June 1903, *Abrams 3740* (S); Cuyamaca Lake, 23 June 1903, *Abrams 3832 (3822)* (M, G, S, US); Cuyamaca Lake, 23 June 1903, *Abrams 3831* (M, S, US); La Jolla, 16 April 1904, *Chandler 5157* (S); Descanso, 24 May 1906, *T. S. Brandegee* (C); May 1906, *K. Brandegee* (C); May 1906, *G. B. Grant 6850* (S); Point Loma, 21 April 1913, *Eastwood 2862* (CAS); old clearing, La Jolla, 8 March 1914, *Clements & Clements 6* (ANSP, C, F, G, M); Green Valley, 30 May 1915, *Collins & Kempton 149* (G, US); 19 April 1916, *M. F. Spencer 146* (C, G, P, US); Balboa Park, 14 May 1917, *Street* (P); 10 miles east of Campo, 10 June 1917, *McGregor 939* (S); El Granito Springs, 10 April 1918, *Carlson* (CAS); Cuya-

maca Dam, 20 June 1918, *McGregor* (S); Cuyamaca, 25 June 1919, *Eastwood 9132* (CAS); Descanso, 26 June 1919, *Eastwood 9183* (CAS); Laguna Mts., 28 June 1919, *Eastwood 9195* (CAS); Campo, 23 April 1920, *Eastwood 9462* (CAS); Dead Man's Hole, near Warner's Hot Springs, 1 May 1925, *Jaeger* (C, P); near Fallbrook, 750 ft. alt., 15 May 1920, *Munz 3889* (P); 10 miles north of Descanso, 27 June 1923, *Harwood & Munz 7166* (P); near Doane Valley, Palomar Mts., 4800 ft. alt., 22 June 1924, *Munz 8272* (P); near Laguna Camp, Laguna Mts., 25 June 1924, *Munz 8360* (G); Fallbrook, 21 March 1925, *Jaeger* (P); between Escondido and Rincan, 19 April 1925, *Cernman* (OAC); Dead Man's Hole, near Oak Grove, 1 May 1925, *Jaeger* (C, P); Cuyamaca Lake, 4750 ft. alt., 18 May 1925, *Munz 9778* (CP, P); Cuyamaca Lake, 4750 ft. alt., 18 May 1925, *Munz 9777* (C, P); hillside on Banner Grade, 3500 ft. alt., 18 May 1925, *Keck & McCully 132* (P); 4–5 miles from Jamul on road to Barrett Dam, 7 March 1926, *Wiggins 1961* (S); Henshaw Dam, 29 May 1926, *M. E. Jones* (S); Laguna Mts., 22 May 1927, *Sanford* (CAS); Witch Creek, *Alderson* (C); WITHOUT LOCALITY—*Hartweg 1666* (G); 18—, *Bridges 40* (US); Nova Calif., 1833, *Douglas* (G TYPE of *S. humilis* Gray); *Ross* (G); *Fremont's Expedition to California*, 1845–7 (G, US); 1853–4, *Bigelow* (G, US); 18—, *Parry* (M); 1859, *Wallace* (G); 1875, *Vasey* (US); 1879, *Heap* (M); 1880, *Norton* (M); 1880, *Bush* (US); Los Angeles and northward, 1885, *Gray* (G); 1889, *Parry* (M).

MEXICO: LOWER CALIFORNIA—Nachoguero Valley, 1 June 1894, *Mearns 3363* (S, US); northwest of Ensenada, 3 May 1923, *McKeever 31* (G, US); Ensenada, 13 April 1925, *M. E. Jones* (P); 16 miles southeast of Tecate, 12 May 1925, *Munz 9501* (P, S).

In order to clarify the synonymy of this species it is necessary to consider two separate and individual plants, that of the 'Prodromus'[29] and that of the 'Botanical Register.'[30]

De Candolle in the 'Prodromus' gave a very brief description of *Sida malvaeflora* based upon a drawing by Mocino and Sesse in the 'Calques des Dessins'[31] of a plant collected, no doubt, at

[29] DeCandolle, Prod. **1**: 474. 1824.

[30] Lindley in Bot. Reg. **12**: 1036, *pl. 1036*. 1826.

[31] Mocino & Sesse, Calques des Dessins de la Flore du Mexique **1**: *pl. 70*. 1874.

Monterey, California (a blueprint of this is in the Missouri Botanical Garden Library).

Lindley in 1826 applied this name to an Oregon plant collected by David Douglas on the "Multomah" (Multnomah) River, a branch of the Columbia, and stated that it was probably the same plant as that of the 'Prodromus,' which de Candolle "was unable to refer to any certain station in the genus [*Sida*]."

The Douglas plant is conspecific with the *Sidalcea campestris* of Greene,[32] but because of the confused synonymy of that time Greene did not recognize this fact and founded his species on a collection of Howell from "dry prairies" of the Willamette Valley, Oregon, distributed as *S. humilis.* As *S. campestris* is restricted to the Willamette Valley, then without doubt the *Sida malvaeflora* of Torrey and Gray, and of Hooker and Arnott from the "Wahlamet and Umptqua" Valleys is conspecific. However, Dr. Gray[33] in 1849 erroneously combined *S. campestris* with *S. oregana* but he corrected this error in 1887.[34]

When Dr. Gray[35] proposed the genus *Sidalcea* he described *S. humilis,* based on collections of Douglas, Fremont, and Hartweg, from the coastal regions of California, and a Russian collection about San Francisco Bay. At the same time he described *S. delphinifolia,* based as he inferred on *Sida delphinifolia* of Nuttall. Later he[36] gave the name *Sidalcea malvaeflora* to plants which he thought were the same as those of the 'Prodromus,'[37] but Gray's description applies to *S. neo-mexicana* as already used for a species of the inland regions. At this time Gray realized that his *Sidalcea delphinifolia* was not the *Sida delphinifolia* of Nuttall, so he named it *S. hirsuta,* saying that Nuttall's species might be the same as *S. malvaeflora* of the coastal region. Greene[38] did not know of this case of mistaken identity and in his 'Synopsis' still confused *S. malvaeflora* with *S. neo-mexicana* and retained *S. humilis* of Gray for the coastal form. In 'Flora Franciscana'

[32] Greene in Bull. Calif. Acad. Sci. **1**: 76. 1885.
[33] Gray in Mem. Am. Acad. N. S. **4**: 20. 1849 (Pl. Fendl. 20. 1849).
[34] Gray in Proc. Am. Acad. **22**: 286. 1887.
[35] Gray in Mem. Am. Acad. N. S. **4**: 18. 1849 (Pl. Fendl. 18. 1849).
[36] Gray in Smiths. Contr. **3**: 16. 1852 (Pl. Wright. **1**: 16. 1852).
[37] DeCandolle, Prod. **1**: 474. 1824.
[38] Greene in Bull. Calif. Acad. Sci. **1**: 75. 1885.

Greene[39] kept *S. delphinifolia* as the valid name for *S. malvaeflora*, and var. *humilis* (Gray) Greene for Gray's *S. humilis* and still used the name *S. malvaeflora* for *S. neo-mexicana*. Greene[38] had formerly said: "It is to be hoped that the *Sida malvaeflora* of Mocino and Sesse of Mexico is really the same thing [i. e. *Sidalcea malvaeflora*] otherwise the name of *S. neo-mexicana* is to be restored to this."

This restoration was made by Gray,[40] concerning which he says: "M. Alphonse De Candolle, in the preface to the 'Calques des Dessins de la Flore du Mexique de Mocino et Sesse,' several years ago pointed out the fact that the original *Sida malvaeflora* DC. was not the plant of the 'Botanical Register' and not the plant taken up by me as *Sidalcea malvaeflora*. Also I had recognized Mocino's drawing to belong to what I had named *Sidalcea humilis,* the common species of the California coast; . . . . while the other names, *S. neo-mexicana* and *S. oregana* of Pl. Fendl., come into use for the interior country species."

If, then, the name *Sidalcea malvaeflora* is maintained for the species of the coastal region and outer coast ranges from Oregon to Lower California, and other names retained for the more inland species as given above, although the range may be extended northward and southward and slightly eastward, there will be little reason for confusion as to what constitutes the common coastal species. It is a very polymorphic species and shows great variation in the coastal counties. Specimens from Alameda and San Mateo Counties show a very coarse pubescence throughout, those from Santa Clara County a delicately cleft leaf form, whereas those from San Diego County are almost scurfy due to the shortness and puberulence of the hairs, although others are almost glabrous, described as "glabriuscula" in the 'Prodromus.'

Sidalcea rostrata of Eastwood is a less-cut leaf form; and, as all young carpels are "rostrate" and the other characters given in the original description of this species apply to the low more decumbent forms of the middle-coast region, it seems best to treat this merely as a local variant of the species.

[39] Greene, Fl. Francis. 105. 1891.
[40] Gray in Proc. Am. Acad. **21**: 409. 1886.

Sidalcea scabra of Greene, from the vicinity of Byron Hot Springs, although having less orbicular leaves and a closer, harsher puberulence, has very close relatives in many of the more southern forms. This apparent relationship is probably due to some environmental influence, corresponding to the ecological conditions in the desert region of the south. In dry or sandy regions the plants have a tendency toward close stellate or more radiate hairs, which does not occur in the regions of greater moisture. This is exemplified by the plants from San Mateo and Humboldt Counties, as contrasted with those from the Tehachapi region and the more arid parts of San Diego County.

12a. Var. **californica** (Nutt.) Jepson, Man. Fl. Pl. Calif. 630. 1925.

Sida californica Nutt. in Torr. & Gray, Fl. N. Am. **1**: 233. 1838; Walp. Rep. **1**: 316. 1842. Walp. Ann. **2**: 151. 1851–52.

Sidalcea californica (Nutt.) Gray in Mem. Am. Acad. N. S. **4**: 19. 1849 (Pl. Fendl. 19. 1849); in Proc. Am. Acad. **22**: 286. 1887; Greene, Fl. Francis. 106. 1891; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 30. 1894); Gray, Syn. Fl. N. Am. **1**[1]: 304. 1897; Davidson & Moxley, Fl. S. Calif. 231. 1923.

Velvety stellate-tomentose throughout; stem erect, stout, up to 7.5 dm. high; leaves less deeply lobed than in the species, densely stellate-pubescent on the lower surface, with few-rayed appressed hairs on the upper surface; calyx 3–5-nerved.

Distribution: Santa Inez Mts., Santa Barbara County to Ventura County, California.

Specimens examined:

California: santa barbara county—*Nuttall* (ANSP type of *Sida californica* Nutt.); Santa Inez Mts., near Santa Barbara, (26?) March 1861, *Brewer 337* (C, G, US); Santa Barbara, 13 April 1887, *B. H. Smith* (ANSP); Mission Canyon, Santa Barbara, Feb.–May 1885, *Gray* (G); Santa Inez Mts., 1888, *T. S. Brandegee* (C); Santa Barbara, June 1889, *T. S. Brandegee* (C); Santa Barbara, 189–, *L. G. Yates* (CAS); Montecito, March 1895, *L. G. Yates* (US); Santa Barbara, May 1902, *Elmer 3767* (C, G, M, P, S, US); Santa Barbara, 25 April 1903, *Grant 5452* (C); Mission Canyon, 21 April 1908, *Eastwood 20* (C, F, G, M,

US); among hills south of Lompoc, 14 June 1913, *Suksdorf 182* (G); Santa Barbara, 12 April 1926, *Munz 10327* (CP, P); San Miguelito Canyon, Lompoc, 10 April 1926, *Munz 10271* (P); VENTURA COUNTY—Ojai Valley, 5–8 May 1896, *Hubby* (C, G); Foster Park, Ventura, 14 April 1916, *Eastwood 4976* (CAS).

13. S. reptans Greene in Pittonia **3:** 159. 1897; Hall & Hall, Yosemite Fl. 158. 1912; Smiley in Univ. Calif. Publ. Bot. **9:** 264. 1921.

S. spicata Greene var. *reptans* (Greene) Jepson, Man. Fl. Pl. Calif. 630. 1925.

S. favosa Congdon in Erythea **7:** 183. 1900.

Perennial from a woody tap-root; stems one to several, usually simple, decumbent at the base, creeping and rooting at the nodes, the erect portion up to 6 dm. high, slender, and hirsute; leaves mostly from the basal horizontal portion of the stem, orbicular, 1–7 cm. broad, crenate, coarsely dentate or rarely lobed, the lobes or segments obtuse and mucronate, more or less hirsute on both surfaces, sinus closed or truncate, petiole greatly elongated up to 2.5 dm. long, hirsute; cauline leaves deeply lobed or parted, the segments coarsely dentate or lobed, sinus more open, petioles short; stipules of the basal leaves thin, purplish, almost oblong, those of the cauline leaves ovate and blunt or acute, ciliate; inflorescence few-flowered, racemose, simple or rarely branched; rhachis, pedicels, bracts, and calyx rough with a short-stellate tomentum; bracts simple, often bidentate, oblong or ovate, thickish, ciliate, of equal length with the pedicels; calyx-lobes deltoid-ovate and acute, or ovate-lanceolate and acuminate, margins ciliate and veins hirsute; petals purple, emarginate and denticulate; carpels 8–10, not depressed, favose with extremely short meshes, when young densely stellate-pubescent on the back and the apiculation.

Distribution: in marshes and wet meadows in the Sierra Nevada from Amador County south to San Bernardino County, California.

Specimens examined:

CALIFORNIA: AMADOR COUNTY—Antelope, July 1892, *Hansen 506* (M, ND TYPE, P, S); July 1893, *Hansen 506* (G, US);

23 July 1896, *Hansen 506* (P, US); CALAVERAS COUNTY—18–30 May 1895, *Davy 1505* (G); TUOLUMNE COUNTY—18—, *Chesnut & Drew* (C); Hog Ranch, 8 July 1896, *Congdon 14* (G, S); Mather, 15 July 1922, *H. M. Hall 11809* (C); Mather, 16 July 1923, *Munz 7349* (P); Pine Crest, 4 July 1926, *Pendleton* (OAC); Cold Springs, 10 July 1926, *R. A. Pendleton* (OAC); YOSEMITE NATIONAL PARK—Big Tree Grove, Yosemite Valley, 1860–67, *Bolander* (C, G, US); MARIPOSA COUNTY—Koontz Place, 11 Aug. 1899, *Congdon* (C TYPE of *S. favosa* Congdon); MADERA COUNTY—Shuteye Mountain, 9 Sept. 1907, *Murdoch 2512* (G, US); FRESNO COUNTY—Pine Ridge, 15, 25 June 1900, *Hall & Chandler 166* (ANSP, C, M, US); TULARE COUNTY—General Grant Grove, 20 July 1892, *T. S. Brandegee* (C); Grant Park, 11 Aug. 1895, *Dudley 1199* (S); SAN BERNARDINO COUNTY—near Bear Valley, July 1899, *Hall 1325* (C); Bear Valley, San Bernardino Mts., 19 July 1900, *M. E. Jones 6209* (P, S); Aug. 1900, *Shaw & Illingsworth 51* (S); Bear Valley, San Bernardino Mts., 2 Aug. 1902, *Abrams 2860* (ANSP, CAS, C, G, M, P, US); 2 miles east of Bluff Lake, 1 July 1926, *Munz 10572* (C, P); WITHOUT LOCALITY—Ellis Meadows, *K. Brandegee* (C); July 1908, *Davidson* (S); Round Mt., 30 June 1901, *Hopping 177* (C); near Jackass Meadows, Upper San Joaquin, 16 Aug. 1895, *Congdon 27* (G); General Grant National Park, 4 July 1927, *Jessel* (CAS).

No definite characters appear in the specimens from San Bernardino County, previously referred either to *S. malvaeflora* or *S. neo-mexicana,* to separate them from *S. reptans.*

Sidalcea favosa Congdon[41] differs in no essentials from *S. reptans.* With the exception of "stems decumbent," Congdon's description corresponds equally well to that of Greene for *S. reptans.*

14. **S. asprella** Greene in Bull. Calif. Acad. Sci. **1**: 78. 1885; Gray in Proc. Am. Acad. **22**: 286. 1887; Greene, Fl. Francis. 106. 1891; E. G. Baker in Jour. Bot. **29**: 52. 1891 (Synopsis Malveae, 30. 1894); Gray, Syn. Fl. N. Am. **1**^{1}: 305. 1897, in part; Hall & Hall, Yosemite Fl. 157. 1912; Smiley in Univ. Calif. Publ. Bot. **9**: 265. 1921, as to name only.

[41] Congdon in Erythea **7**: 183. 1900.

S. malvaeflora (DC.) Gray var. *asprella* Jepson, Man. Fl. Pl. Calif. 630. 1925.

S. elegans Greene in Cyb. Columb. **1:** 35. 1914.

Perennial from a slender horizontal root, roughish throughout with a short stellate pubescence or almost scurfy-puberulent; stems several, slender, procumbent or erect, up to 7.5 dm. high, simple or branched, leafy up to the inflorescence; all leaves similar in shape, orbicular to semi-orbicular, differing only in size, 1–10 cm. broad, cleft about halfway to the base, the lobes subentire, crenate or irregularly and coarsely dentate; stipules lance-linear or subulate; inflorescence slender, racemose, few-flowered, up to 4.5 dm. long; rhachis, bracts, pedicels, and calyx densely stellate-pubescent; bracts bifid, very minute; calyx accrescent, the lobes ovate or triangular-lanceolate, acute, prominently 3-nerved; petals purple, as much as 2.5 cm. long; carpels large, transversely rugose-reticulate, slightly angulate.

Distribution: western Oregon and hillsides of the lower Sierra Nevada south to southern California.

Specimens examined:

OREGON: MARION COUNTY—Silverton, June 1882, *T. Howell 603* (G); LANE COUNTY—near Coburg, Willamette Valley, 4 May 1887, *T. Howell* (C, ND, S); DOUGLAS COUNTY—Oakland, 1874, *Nevins* (US); Glendale, 30 June 1887, *T. Howell 733* (G); Glendale, 19 June 1902, *M. E. Jones* (P); Riddle, 26 June 1913, *Peck 6853* (Wil.); Rogue River Canyon near Mule Creek, 27 June 1917, *Peck 6846* (Wil.); 3 miles northeast of Gunter, 1100 ft. alt., 19 June 1919, *J. C. Nelson 2678* (G); Dillard, 10 miles south of Roseburg, 4 July 1927, *J. W. Thompson 2035* (S); Camas Valley, 3 June 1928, *Thompson 4446* (M); just north of Oakland, 2 June 1928, *Thompson 4389* (M); CURRY COUNTY—2 miles south of Illahe, 21 June 1917, *J. C. Nelson 1360* (G); above Agness, 22 May 1929, *Henderson 10149* (O); Tolman Ranch, up Chetco River 20 miles, 5 July 1929, *Leach & Leach 2422* (O); near Carpenterville, 14 July 1929, *Henderson 11357* (O); JOSEPHINE COUNTY—Grant's Pass, 12 June–11 July 1886, *Henderson 149* (ANSP, C, OAC); dry pine woods, Grant's Pass, 20 June 1886, *Henderson* (O); Grant's Pass, 1886, *Henderson 37* (G); Grant's Pass, 26 June 1886, *Henderson* (O); Eight Dollar Mt., 12 June

1904, *Piper 6171* (US TYPE of *S. elegans* Greene); Grant's Pass, 24 June 1909, *Peck 6878* (Wil.); Grant's Pass, 6 May 1912, *Prescott* (G, S, Wil.); Pacific Highway, 12 May 1924, *Abrams & Benson 10424* (S); near Waldo, 25 April 1926, *Henderson 5998* (CAS, M, O, RM, S); base of Eight Dollar Mt. near Selma, 19 June 1926, *Henderson 7233* (O); 10 miles southwest of Waldo, 7 June 1928, *Thompson 4584* (M); JACKSON COUNTY—near Wimer, 28 May 1892, *Hammond 59* (US); near Elk Creek, 3000–4000 ft. alt., *Applegate 2568* (US); Lower Applegate Creek, 700 ft. alt., 17 June 1899, *Leiberg 4098* (US); Trail, 2 June 1924, *Sherwood 831* (Wil.); Jackson Creek, ¾ mile west of Jacksonville, 10 May 1924, *Abrams & Benson 10245* (S); WITHOUT DEFINITE LOCALITY—1871, *E. Hall 71* in part (M); southern Oregon, 1893, *Durden* (C); head of Coos River, 3 Sept. 1911, *House 4835* (US).

CALIFORNIA: DEL NORTE COUNTY—Douglas Park, 9 miles east of Crescent City on Grant's Pass Road, 4 July 1926, *Kildale 2280* (S); Siskiyou Mts., Sept. 1885, *T. S. Brandegee* (C); grade east of Gasquets, 3 July 1899, *Dudley* (S); near Gasquets, 27 June–1 July 1922, *Abrams 8506* (P, S); Shelley Creek, 6 Aug. 1923, *Eastwood 12080* (CAS); Gasquets, 10 Aug. 1923, *Eastwood 12226* (CAS); Douglas Park, 5 June 1928, *Thompson 4507* (M); HUMBOLDT COUNTY—Willow Creek, May 1883, *Rattan* (G); Arcata Trail via Willow Creek, June 1883, *Rattan* (S); Klamath River, 1400 ft. alt., June 1901, *Chandler 1466* (C); Klamath River, 1000 ft. alt., June 1901, *Chandler 1438* (C); valley of Van Duzen River opposite Buck Mt., 1500 ft. alt., 27 June–30 July 1908, *Tracy 2813* (C, G, US); along road between Three Creeks and mouth of Willow Creek, about 2500 ft. alt., 6 July 1911, *Tracy 3349* (C, G, US); near Hydesville, 100–300 ft. alt., 11 May 1912, *Tracy & Babcock 3598* (C); Horse Mountain, about 5000 ft. alt., 20 June 1926, *Tracy 7659* (C); SISKIYOU COUNTY—Mount Shasta & vicinity, 13–27 July 1892, *Palmer 2519* (US); Sisson, 15 July 1902, *Setchell & Dobie* (C); Mount Shasta, Sept. 1902, *G. B. Grant 5144* (C); near Shasta Springs, 5 June 1905, *A. A. Heller 7987* (M, S, US); McCloud, 15 July 1912, *Eastwood 1101* (CAS, G, M); McCloud, 15 July 1912, *Eastwood 1115* (CAS, US); near Sisson, 22 June 1916, *A. A. Heller 12423* (CAS, F, G, M,

OAC, S, US); Shasta Springs, 2 Sept. 1917, *Eastwood 6692* (CAS, US); Bigelow's, McCloud River, 25 July 1921, *Eastwood 10805* (CAS); Bear Spring, on road to Medicine Lake, 29 July 1921, *Eastwood 10977* (CAS, G); Shasta Springs, 21 May 1923, *Eastwood 11883* (CAS); near Dunsmuir, April 1925, *Reinoehl* (S); TRINITY COUNTY—Mad River, 1 July 1890, *Price* (C); Upper Mad River, 26 June 1893, *Blankinship* (C); summit between Mad and Trinity Rivers, on Eureka-Red Bluff Road, 22 July 1916, *Abrams 6193* (S, US); SHASTA COUNTY—near Redding, 27 May 1905, *A. A. Heller 7876* (ANSP, C, F, G, M, S, US); Redding, 30 April 1910, *W. W. Jones 130* (G); Montgomery Creek, 27 June 1912, *Eastwood 671* (CAS, G, US); Goose Valley, 29 June–11 July 1912, *Eastwood 754* (CAS, G, US); Redding, 24 May 1913, *L. E. Smith 243* (G, US); Goose Valley, 29 June–8 July 1912, *Eastwood 952* (CAS, US); Burney, 28 June 1912, *Eastwood 704* (US); Burney, 17 June 1923, *Bethel* (CAS); BUTTE COUNTY—Mt. Ida Ranch, 10 miles east of Oroville, 25 May 1915, *A. A. Heller 11898* (CAS, F, G, M, OAC, S, US); YUBA COUNTY—near Camptonville, 1 July 1884, *Greene* (G COTYPE); near Los Vergils Dam, 22 May 1921, *Eastwood* (CAS); NEVADA COUNTY—between Grass Valley and Nevada City, 14 July 1905, *A. A. Heller 8105* (ANSP, G, M, US); west of Grass Valley, 24 May 1919, *A. A. Heller 13189* (ANSP, CAS, F, G, M, S, US); Nevada City, 20–22 June 1912, *Eastwood 617* (CAS, G, M, US); near Grass Valley, about 850 m. alt., 7 June 1916, *Hall & Essig 242* (*10163*) (C, CAS, M, P, S, US); PLACER COUNTY—Little Bear Valley, 8 Aug. 1909, *Dudley* (S); 8 miles east of Colfax, 19 June 1917, *A. A. Heller 12744* (ANSP, CAS, G, OAC, S, US); ELDORADO COUNTY—rocky places, 22 May 1903, *Gross* (S); Simpson's Ranch, Sweetwater, May 1907, *K. Brandegee* (ANSP, CAS, G, M, P, US); Sweetwater Creek, 14–20 May 1907, *K. Brandegee* (C); Simpson's Ranch, Sweetwater Creek, 19 May 1907, *K. Brandegee* (C); Sweetwater Creek, 20 May 1907, *K. Brandegee* (C); Simpson's Ranch, Sweetwater Creek, 20–28 May 1907, *K. Brandegee* (C); Colfax Road, above Bear River, 2800 ft. alt., 23 May 1926, *L. S. Smith 1842* (CAS); AMADOR COUNTY—24 May 1886, *Curran* (C); 10 June 1889, *Greene* (C, ND); 1891, *Hansen* (C); Agric. Station (cultivated ?), 2000 ft. alt., May 1893.

Hansen 78 (C, M, OAC, P, S, US); near Jackson, 1600 ft. alt., 1–20 June 1904, *Mulliken 109* (C, S); CALAVERAS COUNTY—Mokelumne Hill, *Blaisdell* (CAS, US); Murphy's, 17 May 1887, *B. H. Smith* (ANSP); Big Tree Grove, 23–25 July 1884, *Ball* (US); Calaveras Ranger Station, Stanislaus Forest, Avery, 1000 ft. alt., 26 May–8 June 1913, *Eggleston 9132* (US); valley three miles west of Avery, 3100 ft. alt., 23 May 1921, *Tracy 5713* (C); Angel's Camp, 11 April 1923, *Eastwood 11655* (CAS); about 2½ miles east of Murphy, about 2800 ft. alt., 21 May 1927, *Stanford 416* (CP); MARIPOSA COUNTY—Whitlock's, 16 May 1897, *Congdon* (C, S); Mt. Buckingham, 28 May 1898, *Congdon* (C); Whitlock's, 24 May 1903, *Congdon* (US); TUOLUMNE COUNTY—Priest's, 21 May 1899, *Congdon* (CAS, S); Sonora, 520 m. alt., 21 May 1913, *Eggleston 9077* (US); Camp Baxter, 5500–5700 ft. alt., 30 June 1929, *Stanford 1083* (CP); TULARE COUNTY—Giant Forest, 1908, *G. R. Hall* (P); SAN BERNARDINO COUNTY—7 Oaks Camp, San Bernardino Mts., 11–14 June 1901, *G. B. Grant* (S).

This species as originally delimited had a very limited longitudinal range in the lower altitudes of the Sierra Nevada. It has often been confused with *S. glaucescens*, but the longer stellate pubescence, non-glaucous surfaces, usually more erect habit, and form of leaves separate it from those glaucescent forms of higher altitudes. The type specimens of these two species are similar only in habit of growth.

Sidalcea elegans Greene, the type locality of which is Josephine County, Oregon, is conspecific with *S. asprella*, and therefore the range of this species is extended farther north. In some of the Oregon specimens, referable to *S. elegans*, the inflorescence is more slender, the leaves are mostly basal, and many of the plants are almost vine-like in habit.

15. S. robusta Heller, n. sp.[42]

[42] **Sidalcea robusta** Heller, nov. sp., perennis; caule robusto, erecto, 9–12 dm. alto, glauco, glabro; foliis inferioribus orbiculato-cordatis, usque ad 6 cm. latis, 7-partititibus, subtus cinereo-stellatis, segmentis cuneatis tri-lobatis et acuto-dentatis; foliis caulis palmato-divisis in segmentis linearibus plus minusve integris; inflorescentia laxe racemoso usque ad 4.5 dm. longo; rhachiis, bracteis, pedicellis calyceque dense stellato-tomentosis; bracteis simplicis, lanceolatis, acutis, lobis calycis ovato-lanceolatis, acuminatis, prominente tri-nerviis; corollis pallido-purpurascentibus usque ad 3 cm. longis; carpellis ignotis.—Collected along Chico Creek, 5 miles east of Chico, California, 17 May 1915, *A. A. Heller 11879* (Herb. of A. A. Heller TYPE).

Perennial from an apparently creeping rootstock; stems stout, erect, 9–12 dm. high, simple or nearly so, often scape-like, somewhat glaucous, nearly glabrous or hirsute at the base, sparingly leafy; basal leaves orbicular-cordate, up to 6 cm. broad, parted almost to the base into about 7 more or less 3-lobed and sharply toothed cuneate segments, the upper surface with appressed simple or geminate hairs, the lower surface pale ashy gray with short stellate hairs, the petioles shortly stellate; cauline leaves parted almost to the base into lanceolate or linear, entire or slightly dentate segments, pubescence as for the basal leaves; inflorescence loosely racemose, up to 4.5 dm. long; rhachis, bracts, pedicels, and calyx densely stellate-tomentose; bracts simple, lanceolate, acute; calyx-lobes ovate-lanceolate, acuminate, prominently 3-nerved; petals pale lilac, turning dull or yellowish when dry, large, up to 3 cm. long, only slightly retuse; mature carpels not seen.

Type specimen: *A. A. Heller 11879* in Heller Herbarium.

Distribution: on the bluffs above Chico Creek, near Chico, and in Berry Canyon near Clear Creek, Butte County, California.

Specimens examined:

California: butte county—*Fremont's 3rd Exped. 356* (US); Chico Ranch, May 1879, *Bidwell* (G); 28 April, *Gray* (G); Little Chico Canyon, April 1896, *Austin 822* (C, M, US); Little Chico Creek, May 1896, *Austin 674* (M); Little Chico Creek, 5 June 1897, *Austin 1920* (US); Little Chico, May 1898, *Bruce 1920* (P); Forest Ranch, May 1898, *Bruce 2390* (P); Chico, April 1899, *E. B. Copeland* (S); Berry Canyon, near Clear Creek, 8 May 1902, *A. A. Heller & Brown 5496* (ANSP, F, G, M, P, S, US); volcanic uplands along Chico Creek, 5 miles east of Chico, 17 May 1915, *A. A. Heller 11879* (CAS, F, G, M, OAC, US, cotypes).

Sidalcea robusta, although conspicuously unlike the majority of specimens of *S. asprella*, nevertheless is very closely related to that species and may eventually be combined with it as a variety. In default of experimental work or transplants of this restricted group and because of the lack of mature fruits it can not at present be referred to *S. asprella*. Many similarities, however,

may be found between Butte County specimens and some of the collections from near Redding, Shasta County.

16. S. glaucescens Greene in Bull. Calif. Acad. Sci. **1:** 77. 1885; Gray in Proc. Am. Acad. **22:** 287. 1887; Greene, Fl. Francis. 106. 1891; E. G. Baker in Jour. Bot. **29:** 52. 1891 (Synopsis Malveae, 31. 1894), excluding synonymy; Gray, Syn. Fl. N. Am. **1**[1]: 306. 1897, excluding synonymy; Howell, Fl. N. W. Am. 101. 1897, as to California specimens only; Jepson, Man. Fl. Pl. Calif. 631. 1925.

S. montana Congdon in Erythea **7:** 183. 1900.

Perennial from a strong woody root, glaucous and seemingly glabrous throughout or with a sparse minutely stellate puberulence; stems several, slender, procumbent (often appearing vine-like) or erect, up to 7.5 dm. long; all leaves similar, 1–6 cm. broad; basal leaves deeply lobed or palmately parted; cauline leaves palmately 5–7-parted into narrowly cuneate, 3–5-lobed, or dentate segments, those of the uppermost leaves lance-linear and entire; inflorescence a slender loosely flowered raceme frequently 3 dm. long; bracts, pedicels, and calyx usually somewhat stellate-pubescent; bracts small, simple and subulate or deeply bifid; calyx-lobes attenuate, acuminate, becoming broadened at the base and much veined after anthesis; petals deep purple, obovate, entire, or retuse and denticulate; carpels large, reticulate, the reticulations somewhat elongated dorsally.

Distribution: higher Sierra Nevadas of California from the Lassen Butte region southward to Mariposa County.

Specimens examined:

California: lassen butte region—Battle Creek meadows, 22–26 Aug. 1912, *Eastwood 1919* (CAS, G, M, US); Morgans Springs, 22–26 Aug. 1912, *Eastwood 1757* (CAS, M, US); plumas county—May 1877, *Austin* (M, US); Big Meadows, 25 July 1882, *Cleveland* (C); Prattville, 3 July 1892, *T. S. Brandegee* (C); Mt. Hough, 1760 m. alt., Aug. 1901, *Eggleston 7695* (US); July 1918, *Sutliffe* (CAS); Greenville, 9 June 1920, *M. S. Clemens* (CAS); Quincy, 29 June 1920, *M. S. Clemens* (US); Forest Lodge, Greenville, 12 June 1927, *Eastwood 14504* (CAS); butte county—Iron Canyon, May 1896, *Austin 133* (M, ND, US); on road from

Prattville to Chico, at Jonesville, 9 July 1897, *M. E. Jones* (P); summit east of Jonesville, 7000 ft. alt., 7 Aug. 1914, *A. A. Heller 11656* (C, CAS, G, M, OAC, S, US); SIERRA COUNTY—summit of Ebbetts Pass, 7 Sept. 1926, *Ferris 6846* (S); NEVADA COUNTY—Soda Springs, 27 July 1881, *M. E. Jones 2556* (P, S); Truckee, Aug. 1884, *Sonne 63* (M); Soda Springs, 27 July 1881, *M. E. Jones 2556* (P, S); near Summit Station, Donner Pass, 27 July 1903, *A. A. Heller 7047* (ANSP, C, G, M, P, S, US); Donner, Summit Station, 15 July 1908, *K. Brandegee* (C); Truckee, 2100–2600 m. alt., 15 June 1913, *A. E. Hitchcock 370* (US); Truckee River near Boca, 1913, *K. Brandegee* (C); PLACER COUNTY—Summit Valley, Aug. 1883, *Greene* (G, F); Summit, Aug. 1884, *Greene* (G COTYPE ?); Summit Station, Oct. 1887, *Parry* (M); road to Lake Tahoe, July 1888, *Sonne* (US); Truckee, canyon above Coldstream, 31 July 1892, *Sonne 42* (M); Aug.–Oct. 1892, *Carpenter 45* (C, US); 1893, *Hardy* (C, US); Summit, Sierra Nevada Mts., 7000 ft. alt., 26 July 1900, *M. E. Jones* (P); Tahoe Tavern, Lake Tahoe, 15 July 1906, *G. B. Grant 7068* (S); Cisco, 5940 ft. alt., 25 July 1908, *Walker 1388* (C); Cisco, 6000 ft. alt., 1 July 1910, *H. M. Hall 8732* (C, US); Old Cisco, along Yuba River, 5700 ft. alt., 11 July 1910, *H. M. Hall 8758* (S); Tahoe City, 15–19 June 1912, *Eastwood 466* (CAS, US); Summit, 9 Aug. 1913, *Smiley 452* (G); LAKE TAHOE REGION—31 Aug. 1872, *Redfield 40* (C, M); Lake Tahoe, 1 Aug. 1891, *W. H. Evans* (M); Lake Tahoe, June 1906, *G. B. Grant 1098* (C); Squaw Creek, 1909, *Eastwood 237* (CAS); Tahoe Camp, Lake Tahoe, 6800 ft. alt., 25 June 1928, *Munz 11091* (M); Mt. Tallac, Aug. 1906, *Eastwood 1021* (CAS, US); ALPINE COUNTY—Hermit Valley, 1877, *Hooker & Gray* (G); Hermit Valley, 8000 ft. alt., Aug. 1903, *Hall & Chandler 4772* (C); AMADOR COUNTY—Bear River, 5500 ft. alt., 30 Aug. 1896, *Hansen 1954* (M, S, US); CALAVERAS COUNTY—Big Trees, June 1889, *Greene* (C); Calaveras Big Tree Grove, 4 July 1891, *T. S. Brandegee* (C); near Big Tree Grove, Aug. 1906, *Dudley* (S); Salt Spring Reservoir, June 1923, *Steinbeck* (CAS); YOSEMITE NATIONAL PARK—Big Tree Road, near Camp 129, 30 July 1863, *Brewer 1949* (US); Crane Flat, 3 Sept. 1907, *Eastwood 725* (CAS); Tioga Road near Aspen Valley, 8 Aug. 1907, *Eastwood 167* (CAS, US); Tioga Road near Dark Hole, 7700 ft. alt.

23 Aug. 1916, *Smiley 884* (G); TUOLUMNE COUNTY—Williams Ranch, 14 June 1895, *Blasdale* (C); Pine Crest, 4 July 1926, *Pendleton* (OAC); MARIPOSA COUNTY—east of Minarets, alt. 11000 ft., 22 Aug. 1899, *Congdon* (C TYPE of *S. montana* Congdon); WITHOUT LOCALITY—near Donner Lake, 1865, *Torrey 54* (G); dry granite ledge, Black Rock Mts., 7000 ft. alt., 5 Aug. 1900, *Leiberg 5284* (US); near Bald Hill, 6000 ft. alt., 8 July 1900, *Leiberg 5061* (US); Sunnyside, 1909, *Eastwood 36* (CAS); near top of Bear Ridge, 7000 ft. alt., 23 July 1921, *Head* (CAS).

The range of *S. glaucescens* has previously been given[43] as extending to Victoria, British Columbia, and Antelope Island, Utah; however, the former plants are *S. Hendersoni* and the latter *S. neo-mexicana* or *S. oregana.* The plants from Victoria are mostly pistillate, bright green in foliage, and have no glaucescence, and thus are referable to *S. Hendersoni.*

The type specimen of *S. montana* of Congdon, although collected at 11,000 feet east of the Minarets in Mariposa County, from 3000–5000 feet above the usual range of *S. glaucescens,* undoubtedly belongs here, though H. M. Hall[44] placed it temporarily under *S. asprella,* at the same time questioning the relationship of *S. asprella* and *S. glaucescens.* The cut of the leaves, the laxly decumbent habit, glaucous appearance, and stellate puberulence are those of *S. glaucescens.* This therefore reduces the range of *S. asprella* as given by F. J. Smiley[45] in his discussion of plants of the boreal regions of the Sierra Nevada. Although these two species, *S. asprella* and *S. glaucescens,* have a somewhat similar longitudinal range, *S. glaucescens* occurs at higher altitudes than *S. asprella,* is glaucous (often minutely puberulent), and the leaf segmentation is more constantly similar. *Sidalcea asprella* extends farther coastward and northward.

17. S. multifida Greene in Cyb. Columb. **1:** 34. 1914; Tidestrom in Contr. U. S. Nat. Herb. **25:** 353. 1925. Pl. 12, fig. 1.

Caespitose perennial from a somewhat horizontal woody root, pale glaucous, and minutely stellate-puberulent throughout;

[43] Gray, Syn. Fl. N. Am. 1^1: 306. 1897.

[44] Hall, in Univ. Calif. Publ. Bot. **4:** 200. 1912.

[45] Smiley, A report upon the boreal flora of the Sierra Nevada of California. Univ. Calif. Publ. Bot. **9:** 265. 1921.

stems mostly several, slender, erect, up to 4.5 dm. high; leaves mostly basal, 1–5 cm. broad, all deeply 5–7-parted into 2–5-lobed cuneate segments, the lobes oblong to linear; uppermost cauline leaves similar but the segments mostly entire or linear; stipules lanceolate, ciliate; inflorescence few-flowered, racemose; rhachis, bracts, and pedicels minutely stellate-puberulent; bracts short, ovate, simple or bidentate or bifid; calyx densely close stellate-tomentose, lobes lanceolate, acuminate; petals purple, large, up to 2 cm. long, denticulate and retuse; carpels purplish, usually 5, delicately reticulate.

Distribution: vicinity of Reno and in the foothills of the Peavine Mts., Nevada.

Specimens examined:

Nevada: washoe county—Reno, foothills, 6000 ft. alt., 9 June 1897, *M. E. Jones* (M, P, S, US type); Reno, 4500 ft. alt., 8 June 1897, *M. E. Jones* (P); Peavine Mountains, 2 June 1909, *A. A. Heller 9716* (ANSP, G, S, US); Peavine foothills, near Reno, 8 June 1913, *K. Brandegee* (C); Reno, 1350–1500 m. alt., 18 July 1913, *A. E. Hitchcock 549* (US); storey county—near Virginia City, 1864, *Bloomer* (US); Virginia, 7000 ft. alt., June 1905, *McDermott 1514* (US); ormsby county—near Carson City, 1864, *Anderson 77* (G); on slopes, Callahan's ranch north of Carson City, 1650 m. alt., 16 July 1919, *Tidestrom 10562* (G, US); lander county—Galena Creek, 2400 m. alt., 17 July 1919, *Tidestrom 10569* (US); Galena Creek, 2400 m. alt., 17 July 1919, *Tidestrom 10571* (US).

This species may easily be confused with *S. glaucescens*, if specimens farthest from the type locality be examined. However, the caespitose habit, much more pedately parted leaves, the more upright, slender, scapiform stems, and large purple flowers readily separate it specifically from the more "trailing" forms of *S. glaucescens*. The contrast of glaucous leaves and purple flowers makes this one of the most beautiful species in the genus.

18. S. pedata Gray in Proc. Am. Acad. **22**: 288. 1887; E. G. Baker in Jour. Bot. **29**: 53. 1891 (Synopsis Malveae, 31. 1894); Gray, Syn. Fl. N. Am. **1**[1]: 306. 1897. Pl. 12, fig. 2.

S. spicata Greene var. *pedata* (Gray) Jepson, Man. Fl. Pl. Calif. 630. 1925.

Subacaulescent perennial from a tuberous-thickened root, more or less purplish throughout; stems single or clustered, exceedingly short; leaves from the apex of the short stem, 1–5 cm. broad, sparsely or evidently hirsute on the petioles and both surfaces, all similar, pedately parted into narrow cuneate, 2–3-lobed segments, the lobes linear or oblong, entire; inflorescence subscapiform, up to 4.5 dm. long, 1–2-leaved and more or less hirsute, especially toward the base; raceme many-flowered, at length elongated; rhachis, short pedicels, and bracts sparsely and minutely stellate-pubescent; bracts simple, bidentate or bifid, subulate and ciliate; calyx-lobes lanceolate, becoming deltoid after anthesis; petals purple, small, narrow, 2–4 mm. wide, emarginate; carpels 5, dorso-laterally rounded, smooth and glabrous.

Stamineal phalanges indistinct, most of the stamens separate but those of the outer series combined more or less at base into threes or fours as in the subgenus *Malvastralcea.*

Distribution: wet places in the vicinity of Bear Valley, San Bernardino Mountains, San Bernardino County, California.

Specimens examined:

California: san bernardino county—wet places, Bear Valley, 6000 ft. alt., June 1886, *S. B. Parish 1805* (C, P, G type, ND, S); Stars Valley, June 1886, *S. B. Parish* (ND); Bear Valley, June 1892, *S. B. Parish* (ND); Bear Valley, 6000 ft. alt., 2 June 1892, *S. B. Parish 2343* (C, F); Bear Valley, 6500 ft. alt., San Bernardino Mts., and their eastern base, June 1894, *S. B. Parish* (M, US); Bear Valley, San Bernardino Mts. and their eastern base, 6500 ft. alt., 19 June 1894, *S. B. Parish 3172* (M, US); Bear Valley, about 6000 ft. alt., 16–20 June 1895, *S. B. Parish 3783* (*3753* ?) (C, CAS, G, ND); Bear Valley, 6600 ft. alt., 19 July 1900, *M. E. Jones* (P); Bear Valley, Aug. 1901, *Shaw & Illingsworth 232* (S); Bear Valley, 3 Aug. 1902, *Abrams 2875* (F, G, M, P); Deer Lick, Deep Creek Valley, 15 June 1906, *Reed* (F); Bear Valley, July 1909, *Davidson 2176* (US); Metcalf Meadow, Bear Valley, 6500 ft. alt., 18 June 1916, *S. B. Parish 10876* (C, S); Bear Valley, 1 June 1917, *Edwards* (P); Bear Valley, 6950 ft. alt., 23 May 1922, *Pierce* (P); low moist ground at east end of Bear Lake, Bear Valley, 6800 ft. alt., 10 June 1922,

Munz 5654 (C, CAS, P); Bear Lake, 24 June 1926, *M. E. Jones* (CAS, S); damp meadow, Bluff Lake, 7400 ft. alt., 4 July 1926, *Munz 10600* (C, P); Baldwin Lake, 19 May 1927, *M. E. Jones* (C, P); San Bernardino Mts., June 1928, *Van Dyke* (CAS).

Restriction to the Bear Valley and Bear Lake region of San Bernardino County, the peculiar rose-purplish shading of colors in the inflorescence, small flowers, the multisect leaves, and the stamineal column make this species very distinct. It may be considered the transition from the subgenus *Eusidalcea*, section *Perennes*, to the subgenus *Malvastralcea* because the stamens, although apparently distinct, are more or less united at the base into three's and four's.

Subgenus II. Malvastralcea Roush

Subgenus II. Malvastralcea Roush, new subgenus.

Suffruticose perennials with the habit of *Malvastrum;* leaves flabelliform (or reniform-orbicular), scarcely or not at all lobed or parted; bracteoles present; stamineal column not conspicuously double, the outer series of stamens combined merely at the base into threes or fours. Sp. 19–19a.

KEY TO THE SPECIES

Pubescence long, soft, stellate; inflorescence loose, few-flowered; bracts lanceolate, small..*19. S. Hickmani*

Pubescence short, rough, stellate; inflorescence congested, many-flowered; bracts broadly ovate, acuminate, large...........*19a. S. Hickmani* var. *Parishii*

19. S. Hickmani Greene in Pittonia **1:** 139. 1887; Fl. Francis. 104. 1891; E. G. Baker in Jour. Bot. **29:** 52. 1891 (Synopsis Malveae, 31. 1894); Gray, Syn. Fl. N. Am. **1**[1]**:** 307. 1897; Jepson, Man. Fl. Pl. Calif. 631. 1925.

Suffruticose perennial from a long woody root, habitally like *Malvastrum;* stems several, up to 4 dm. high, leafy and soft stellate-pubescent throughout; leaves flabelliform or reniform-orbicular, 1–5 cm. broad, crenate, dentate or slightly lobed, with long, soft-stellate pubescence; basal leaves smaller than the middle cauline leaves; stipules narrowly lanceolate or subulate, small, ciliate; inflorescence loosely racemose, few-flowered; rhachis, pedicels, bracts, and calyx densely stellate-villous or stellate-

tomentose; bracts narrowly linear or short and lanceolate, long-ciliate; bracteoles 3, similar to the bracts; calyx membranous or herbaceous, the lobes deltoid, abruptly acute or long-acuminate; petals rose-purple in pistillate flowers, barely 5 mm. long, paler and at least 15 mm. long in the perfect flowers, twisted in drying as in *Sphaeralcea;* carpels glabrous and smooth except for a few transverse wrinkles which may or may not reach the dorsal midvein.

Distribution: Marin and Monterey Counties, California.

Specimens examined:

CALIFORNIA: MARIN COUNTY—Big Carson Ridge, May 1925, *Sutliffe* (CAS); Big Carson Ridge, in burnt area, 7 June 1925, *Eastwood 12995* (CAS, G, P); MONTEREY COUNTY—Reliz Cañon, 1887, *Hickman* (C, ND TYPE); Tassajara Hot Springs, June 1901, *Elmer 3235* (S).

This species and its variety *Parishii* show the most discontinuous distribution in the genus. The species occurs in Monterey and Marin Counties, and the variety occurs only on the west slopes of the San Bernardino Mountains. Future collections may show its occurrence in the intervening area. There is considerable variation within the species, as shown by a comparison of the type with *Eastwood No. 12995,* in which the pubescence is shorter, the bracts smaller, and the calyx lobes are neither as thin nor so acuminate. There is also a tendency in the latter collection toward a lobing of the leaves.

19a. Var. **Parishii** Rob. in Gray, Syn. Fl. N. Am. **1**^{1}: 307. 1897; Jepson, Man. Fl. Pl. Calif. 631. 1925.

Pl. 5, fig. 6; pl. 6, fig. 7; pl. 13, fig. 1

S. Hickmani Greene in Erythea **4**: 65. 1896, not of Pittonia **1**: 139. 1887.

S. Parishii Rob. acc. to Davidson & Moxley, Fl. So. Calif. 231. 1923.

Malvastrum confertum Parish acc. to Jepson, Man. Fl. Pl. Calif. 631. 1925, in synonymy.

Pubescence short, rough, stellate; stipules ovate-acuminate; inflorescence congested, spicate, many-flowered except in the *ecads;* bracts broadly ovate, large, ciliate; bracteoles similar or narrowly lanceolate; calyx-lobes ovate, long-acuminate.

Distribution: San Bernardino Mts., California, between 4600 and 7000 ft. altitude.

Specimens examined:

California: san bernardino county—near Seven Oaks, at 6000 ft. alt., and western slope of Mt. San Bernardino, about 7000 ft. alt., 25 June 1895, *Parish 3786* (C, CAS, G type, ND); Forsee (Foxesee) Creek, and near Seven Oaks, at 6000 ft. alt., 25 June 1895, *Parish 3925* (G, M, SCW); Seven Oaks Camp, 11 June 1901, *Grant 4026* (S); Yucaipa Mts., 4600 ft. alt., 25 June 1909, *F. M. Reed 2755* (C); road crossing Foxesee Creek, 5500 ft. alt., 26 Aug. 1920, *Peirson 2251* (P); Foxesee Creek, dry soil in small clearing, at 6000 ft. alt., 24 June 1922, *Peirson* (P); Foxesee Creek, occasional on dry roadside bank, 5500 ft. alt., 27 Aug. 1922, *Munz 6339* (C, P); recent burn in chaparral, 1 mi. west of Barton Flats, at 5500 ft. alt., 17 July 1924, *Munz & Johnston 8660* (C, P).

This variety is undoubtedly the result of isolation. Although extremely variable, this variation seems to reach its greatest development in two *ecad* forms: *Munz and Johnston No. 8660*, from a burned-over chaparral, is a low suffrutescent *ecad* with a strong tap-root and few, large, lighter-colored flowers, mostly occurring in the leaf axils. This form is due, doubtless, to exposure and little, or deep-seated, moisture. The second *ecad*, represented by *Peirson No. 2251* and *Munz No. 6339* from Foxesee (Forsee) Creek, is probably from a less-exposed place with more available moisture and richer soil. The vegetative growth of the latter *ecad* is conspicuously elongated, the leaves are large and thin, and less puberulent; the inflorescence is also elongated, almost no flowers develop, and the bracts are long and abundant. All gradations from the type to these two *ecads* are shown in the specimens cited.

Subgenus III. Hesperalcea (Greene) Jepson

Subgenus III. Hesperalcea (Greene) Jepson, Fl. West. Mid. Calif. 239. 1901, and ed. 2. 258. 1911; Man. Fl. Pl. Calif. 628. 1925.

§ *Hesperalcea* Greene, Fl. Francis. 106. 1891.

Hesperalcea Greene in Pittonia **2**: 301. 1892; E. G. Baker, Synopsis Malveae, Suppl. 109. 1894.

Suffruticose perennials, habitally unlike any other members of the genus; stems several from a strong woody root, stout and ligneous at the base, leafy and hispidulous, or stellate-hirsute; leaves vitiform; inflorescence glomerate or densely spicate, single or paniculately disposed; calyx accrescent; petals white, deeply notched; stamens few, the outer series apparently separate but usually 2–3-parted, each lobe 1–3-antheriferous. Sp. 20.

20. S. malachroides (H. & A.) Gray in Proc. Am. Acad. **7**: 332. 1868; Brew. & Wats. Bot. Calif. **1**: 83. 1876; Greene in Bull. Calif. Acad. Sci. **1**: 80. 1885; Gray in Proc. Am. Acad. **22**: 286. 1887; Greene, Fl. Francis. 106. 1891; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 30. 1894); Gray, Syn. Fl. N. Am. **1**^{1}: 307. 1897; Jepson, Fl. West. Mid. Calif. 241. 1901, and ed. 2. 260. 1911; Man. Fl. Pl. Calif. 631. 1925.

Pl. 5, figs. 7, 8; pl. 6, fig. 8; pl. 13, fig. 2

S. vitifolia Gray in Proc. Am. Acad. **7**: 332. 1868; E. G. Baker in Jour. Bot. **29**: 51. 1891 (Synopsis Malveae, 30. 1894) (a form with leaves more angulately lobed, shorter and rougher stellate pubescence).

Malva malachroides Hook. & Arn. Bot. Beech. Voy. Suppl. 326. 1840; Torr. & Gray, Fl. N. Am. Suppl. **1**: 681. 1840; Walp. Rep. **1**: 294. 1842; Gray in Mem. Am. Acad. N. S. **4**: 16. 1849 (Pl. Fendl. 16. 1849).

Hesperalcea malachroides Greene in Pittonia **2**: 301. 1892; E. G. Baker, Synopsis Malveae Suppl. 109. 1894.

Perennial; stems several from a strong woody root, erect, up to 1 m. high, stout, leafy-branched above, stellate-hirsute or hispidulous on all younger parts; leaves vitiform, 2–20 cm. broad, palmately veined and lobed, lobes more or less coarsely dentate, upper surface appressed geminate-hirsute, lower surface stellate-hirsute; stipules purplish, lanceolate, membranous, ciliate; inflorescence glomerate or densely spicate, singly or paniculately disposed; rhachis, peduncles, and pedicels geminate- to stellate-hirsute; bracts purplish, simple or bifid, filiform or subulate, ciliate; calyx stellate-tomentose and hirsute, accrescent, mem-

branous and veiny when mature, the lobes often purple at the apex, ovate-lanceolate, acute; petals white, often purplish, oblique, elongate, narrow with a long claw, deeply notched; flowers gynodioecious, outer stamineal phalanges of the perfect flowers 2–3-parted at the summit of the slender column, carpels sometimes present; pistillate flowers about one-third as large as the perfect ones, column short, truncate with few or no anthers; anthers often a delicate heliotrope; carpels dark, 7–9, orbicular-reniform, small, smooth and glabrous, with a prominent dorsal rib when mature.

Distribution: along the coast from southern Oregon to Monterey County, California.

Specimens examined:

Oregon: trail from Ralph's Place to Pistol River, Curry Co., 19 June 1929, *Leach 2421* (O).

California: humboldt county—Redwood Creek, 1878, *Rattan* (S); Mad River, 30 June 1883, *Rattan* (S); 1886, *Marshall* (ND); near Arcata, 8 July 1888, *Chesnut & Drew* (C); Eureka, 17 June 1893, *Blankinship* (C, G); Camp Grant, 13 June 1899, *Davy & Blasdale 5482* (G, P, S, US); Englewood Prairie, 13 June 1899, *Davy 5482* (C); Eureka, 0–500 ft. alt., 4 July 1909, *Tracy 3010* (C); Eureka, 22 May 1910, *Tracy 3141* (C, US); Eureka, 30 June 1912, *Tracy 3716* (C, US); Holmes Flat, 1 July 1918, *Tracy 4964* (C); Eureka, 22 May 1921, *Piper* (CAS); Horse Mountain cut-off, 16 May 1926, *Kildale 1837* (S); Lord-Ellis road, 2 July 1927, *Kildale* (S); mendocino county—Bear Harbor, 1867, *Bolander 6473* (G type of *S. vitifolia* Gray, M, US); Westport, 19 June 1890, *K. Brandegee* (C); Point Arena, 7 July 1892, *Michener & Bioletti 423a* (C); Darle Gulch below Mendocino City, 11 Aug. 1901, *Congdon* (US); Darle Gulch, south of Mendocino, 12 Aug. 1901, *Congdon* (S); Comptche, May 1903, *McMurphy 161* (S); Inglenook Woods, 16 July 1904, *Congdon* (C, M); Gualala River near Mendocino-Sonoma line, 3 July 1920, *Abrams 7604* (S); Westport, 9 July 1923, *Peirson 3774* (P); near Westport, June 1927, *Mrs. E. C. Sutliffe* (CAS, P); monterey county—May–28 June 1893, cultivated at Berkeley (C); near San Francisco, 1868–69, *Kellogg & Harford 106* (M, ND, US); 1–5 May 1904, *Hall 4856* (US); Santa Lucia Mts., 15 June 1893,

Eastwood (US); Slate's near Sur River, 15 June 1893, *Eastwood* (C); Sur Post Office, Mill Creek, May–June 1901, *Davy 7301* (C); Rocky Creek, 4 May 1925, *Ballou* (S); *Bryant* (S); *Abbott* (G); WITHOUT LOCALITY—Nova Californica, 1833, *Douglas* (G TYPE); *Coulter 107* (G); *Anderson* (G); 1860–67, *Brewer* (US); 1869, *Gray* (G); 1872, *Anderson* (*Bolander*) (G); 1875, *Vasey* (US); 18—, *Bioletti* (ND).

Dr. E. L. Greene[46] first made this species a section *Hesperalcea* under *Sidalcea*, then later[47] raised it to generic rank because of its habit, leaf-form, inflorescence, and the cotyledons being abruptly contracted at the base, instead of cordate as in other species. In the most mature seeds available from specimens of *S. malachroides* no very definite evidence was found that the cotyledons are much less cordate than in other species of the genus, although they are more elongate and narrower. This condition is true for all other floral parts and particularly prominent in the petals which are very narrow with a long claw. In the stamineal column there is no indication of the two series of phalanges. Although apparently separate, the few stamens are combined into sets, the outer series mostly 2–3-cleft. Jepson[48] made *Hesperalcea* a subgenus of *Sidalcea*, and although not like other members of the genus in habit the detailed characters are sufficient reason for retaining it in this category.

When Dr. Gray[49] transferred *Malva malachroides* to *Sidalcea* he also described another species, *S. vitifolia*, founded on *Bolander No. 6473*. This form has more angulately lobed leaves, shorter and harsher pubescence, but otherwise is the same as the species.

Specimens cultivated at the University of California from May–June 1893 (C No. 18693, 18694) have leaves 24 cm. broad and a very large and dense inflorescence. If compared with other specimens of this group the influence of habitat may be seen to be a potent factor for variation in size.

[46] Greene, Fl. Francis. 106. 1891.
[47] Greene in Pittonia **2**: 301. 1892.
[48] Jepson, Fl. West. Mid. Calif. 239. 1901.
[49] Gray in Proc. Am. Acad. **7**: 332. 1868.

Horticultural Forms

The following species are reported[50] as cultivated but no specimens were available for examination and the descriptions do not apply to the species as delimited in this study:

S. atropurpurea Hort.
S. campestris Greene.
S. malvaeflora var. *atropurpurea* Hort.
S. malvaeflora var. *Listeri* Hort.
S. mariana Hort.
S. mexicana Hort.

Species Mihi Ignotae

Sidalcea atacosa Buckl. in Proc. Acad. Sci. Phil. **13**: 161. 1862= **Sphaeralcea pedatifida** Gray, Syn. Fl. N. Am. **1**¹: 314. 1897, fide Gray.
Sidalcea nodosa Turcz. in Bull. Soc. Nat. Mosc. I, **36**: 566. 1863.
Sidalcea peruviana Turcz., *ibid.*
Sidalcea triloba Turcz., *ibid.*

List of Exsiccatae

The distribution numbers are printed in *italics*. Unnumbered collections are indicated by a dash. The numbers in parentheses are the species numbers used in this monograph.

Abbott, E. K. — (12); — (20).
Abrams, L. R. *6981, 7498* (1); *7617* (3); *8917* (6); *4772, 8761, 9616, 9676* (7); *732, 9748, 9560* (8); *8716* (9); *3257, 3257a* (11a); —, *1128, 1436, 1602, 2302, 3311, 3740, 3831, 3832, 4225, 6424, 6429, 6921* (12); *2860* (13); *6193, 8506* (14); *2875* (18); *7604* (20).
Abrams, L. R. & G. T. Benson, *10245, 10424* (14).
Aiton, G. B. *62, 1344* (8).
Alderson, R. D. — (12).
Ames, M. E. P. — (4).
Anderson, C. L. *77* (17); — (Bolander, H. N.) (20).
Angier, B. S. —, *90* (12).
Antisell, T. *30* (12).
Applegate, E. I. *58* (8); *2386* (8a); *2568* (14).
Arséne, Bro. G. *18632, 18879* (11).
Atkinson, W. A. — (1); — (12).
Austin, Mrs. R. M. —, *139, 1921* (1); *1924* (2); —, *132* (3); —, *132, 1873, 1922, 11467*, (4); —, *4, 209, 1408, 1659* (7); —, *417, 1660, 2205* (8); *674, 822, 1920* (15); —, *133* (16).
Austin, Mrs. R. M. & Mrs. C. C. Bruce, *1659* (7); *2205* (8).
Bacigalupi, R. *1558* (1); *1152* (12).
Bacigalupi, McMunn & Mason, *1499* (4).
Bailey, V. *552a* (5).
Bailey, W. W. *192* (7).
Baker, C. F. *2931* (1); *2869, 2877, 2963* (4); —, *670, 800, 9180* (5); —, *1168*

[50] Hubbard in Bailey, Stand. Cyc. Hort. **6**: 3162. 1917; Bailey, Man. Cult. Pl. 486. 1924.

(7); *4255* (Coll. Culbertson), *4318* (Coll. Culbertson) (7a); —, *360*, *440*, *461* (11); —, *275*, *611* (12).
Baker, C. F., F. S. Earle & S. M. Tracy, *679* (5); *887* (11).
Baker, M. S. —, *2537* (1); —, *493* (3); —, *148*, *338*, *2343*, *3203c* (7); — (12).
Baker, M. S. & F. Nutting, — (1).
Ball, J. — (14).
Ballou, F. O. — (20).
Barber, E. A. — (5).
Barber, J. H. — (1); — (12).
Barber, M. A. *80* (8a).
Beardslee, H. C. —, *102* (11).
Bentley, G. — (4).
Beschle, Flora — (5).
Bereman, Mrs. *915* (12).
Berg, N. N. — (12).
Bethel, E. — (4); — (14).
Bidwell, Mrs. J. — (2); — (4); — (15).
Bigelow, J. M. — (1); — (2); — (4); — (12).
Biltmore Herb. *3486a* (Colo. Exp. *1–684*) (5).
Bioletti, F. T. — (1); — (12); — (20).
Black, L. A. M. — (7); *67* (8).
Blaisdell, F. E. — (4); — (14).
Blankinship, J. W. — (1); — (4); — (8); — (12); — (14); — (20).
Blasdale, W. C. *1022* (1); — (7); — (12); — (16).
Blockman, I. M. — (12).
Bloomer, H. G. — (17).
Blumer, J. C. *119* (11).
Bolander, H. N. *4813* (1); *6265* (7); *12* (12); —, *4898* (13); *6473* (20).
Booth, Mrs. — (7).
Bowen, W. J. *13* (8).
Bowman, A. M. *55* (1).
Bradshaw, R. V. *1496* (10).
Brandegee, K. — (1); — (3); — (4); — (7); — (7a); — (12); — (13); — (14); — (16); — (17); — (20).
Brandegee, T. S. —, *124* (5); — (7); — (7a); —, *690* (8); *793* (11); — (12); — (12a); — (13); — (14); — (16).
Braunton, E. *182* (12).
Breninger, G. F. — (11).
Brewer, W. H. *1860* (7); *280*, *667*, *1002* (12); *337* (12a); *1949* (16); — (20).
Bridges, T. *40* (12).
Brown, C. L. — (7).
Brown, H. E. *215* (1); *193½* (4); *337* (7); *815* (12).
Browne, A. C. — (12).
Bruce, Mrs. C. C. *1921* (1); *193*, *693*, *1924* (2); *1873*, *1922*, *1923* (B), *2389* (4); *1920*, *2390* (15).
Bryant, W. E. — (20).
Bush, — (12).
Butler, G. D. *905*, *1643*, *1728* (7); *768*, *1408* (8).
Cain, B. C. *72* (7).
Campbell, M. L. — (1).
Cannon, E. — (12).
Carlton, E. C. & A. O. Garrett, *6694* (11).
Carlson, J. — (12).
Carpenter, A. M. — (7); — (16).
Carruth, W. W. — (1).
Carter, W. R. —, *376* (6).
Cary, M. *116* (5); *12* (11).
Cassidy, Prof. — (5).
Cernman, Mrs. — (12).
Chandler, H. P. *7567* (4); *1707* (7); —, *214*, *318*, *529*, *713*, *1020*, *5157* (12); *1438*, *1466* (14).
Chesnut, V. K. & E. R. Drew, — (7); — (13); — (20).
Clark, C. F. — (1).
Clark, J. A. *185* (8).
Claypool, E. V. — (6).
Clemens, Mrs. J. — (5); — (11).
Clemens, M. S. — (6); — (7); — (9); — (16).
Clements, F. E. & E. S. Clements, *6* (12).
Cleveland, D. — (12); — (16).
Clokey, I. W. *3175* (5); *2995* (11).
Cockerell, T. D. A. — (5).
Coghill, G. E. *69* (5).
Coleman, I. — (12).
Collins, G. N. & J. H. Kempton, *149* (12)
Condit, I. J. — (12).
Congdon, J. W. — (1); — (3); — (4); —, *21* (7); —, *14*, *27* (13); — (14); — (16); — (20).
Constance, L. *9685* (8).
Coombs, A. L. — (7).
Copeland, E. B. *3822* (7); *23* (7a); — (15).

Copeland, H. F. *202* (7).
Cotton, J. S. *1330, 1652* (8).
Coues, E. & E. Palmer, —, *221* (11).
Coulter, J. M. — (5).
Coulter, T. *107* (20).
Coville, F. V. *578* (8).
Coville, F. V. & E. I. Applegate, *37* (7).
Coville, F. V. & F. Funston, *1462, 2103* (7a); *954, 1004* (11b).
Coville, F. V. & J. B. Leiberg, *45, 66, 205* (7).
Cowen, J. H. — (5); *82* (11).
Craig, T., V. Newsom, & M. Hilend, *337* (12).
Cramer, C. L. — (8).
Crandall, C. S. —, *81, 107, 201,* (5); —, *108* (11).
Crawford, D. L. — (7a).
Cronkhite, H. M. *82* (7); *61* (8).
Culbertson, see C. F. Baker.
Cummings, C. E. — (11a); — (12).
Curran, M. K. — (1); — (3); — (4); — (7); — (14).
Cusick, W. C. *1668, 2053* (7); —, *1456, 2165, 2831* (8).
Daniels, F. *162* (5).
Davidson, A. *1716* (7a); — (12); — (13); *2176* (18).
Davis, D. D. — (12).
Davy, J. B. *1121, 1330* (1); *6730* (3); *2255, 2336* (11a); *51, 1024, 1101, 2631* (12); *1505* (13); *5482, 7301* (20).
Davy, J. B. & W. C. Blasdale, *5463* (1); *5482* (20).
Detling, R. E. *281* (7).
Douglas, D. — (1); — (9); — (12); — (20).
Drew, E. R., see V. K. Chesnut; — (1); — (12).
Dudley, W. R. — (1); — (7); —, *598, 914, 915, 1721, 1722, 1963, 2303, 2350, 2392, 3013* (7a); — (12); *1199* (13); — (14); — (16).
Dudley, W. R. & F. H. Lamb, *4450* (11a); *4728* (12).
Duncan, C. D. *155* (12).
Duncan, W. B. — (4); — (7a).
Dunn, G. W. — (12).
Durden, Mrs. — (14).
Dutton, H. A. — (1).
Earle, F. S. — (11).
Eastwood, A. *3319, 4586, 12713, 12794, 15158, 15161, 15225* (1); *4392* (2); — (3); —, *602, 10516, 12665,* (4); *12* (5); *62, 1098, 1098a, 1216, 1888, 7821, 7822, 10766, 10964* (7); *13151, 13171, 13390* (8); —, *13, 5919* (11); —, *25, 82, 329, 830, 1608, 2492, 2862, 3244, 9132, 9183, 9195, 9462, 10460, 11807, 13717, 13798, 11465, 14310* (12); *20, 4976* (12a); —, *617, 671, 704, 754, 952, 1101, 1115, 6692, 10805, 10977, 11655, 11883 12080, 12226* (14); *36, 167, 237, 466, 725, 1021, 1919, 14504, 1757* (16); *12995* (19); — (20).
Edwards, — (18).
Eggert, H, — (9).
Eggleston, W. W. *9101* (3); *5868, 10372, 11716, 11958a, 15283* (5); *7031, 7420, 11656* (7); *11388, 12124a, 12698* (8); *5943, 17095* (11); *9077, 9132* (14); *7695* (16).
Elder, J. S. *7, 70, 168* (7).
Ellis, C. C. *214* (5); *244* (11).
Elmer, A. D. E. *4316* (1); *4936* (3); —, *321, 1346* (8); *3569, 4637* (12); *3767* (12a); *3235* (19).
Engelmann, G. — (7); — (11).
Engelmann, H. — (8).
Epling, C. C. — (8); *5322, 5611* (10); *5197, 6224, 6292* (12).
Epling, C. C. & M. Houck, *9186, 9187, 9652* (8).
Epling, C. C. & H. Offord, *8775, 8777* (8).
Evans, H. M. — (7).
Evans, W. H. — (7); — (16).
Evermann, B. W. — (11); — (12).
Faunt le Roy, S. — (4).
Fendler, A. *80* (5); *79* (11).
Fernow, B. E. — (11).
Ferris, R. S. —, *842, 4148* (1); *1279* (11); *1972* (12); *6846* (16).
Ferris, R. S. & R. Duthie, *155, 1062* (7); *35, 154, 720, 843, 1246* (8).
Feudge, J. B. *815, 1159* (12).
Finley, R. C. — (9).
Fletcher, — (6).
Fossler, J. J. — (11).
Foster, A. S. *801* (6).

Fremont's Exp. *432* (1); —, *410* (5); — (11); —, *418* (12); *356* (15).
Fritchey, J. Q. A. *24* (12).
Gabrielson, I. — (8).
Gageby, S. — (8).
Garcia, P. I. *321* (11).
Gardner, N. L. — (6).
Garrett, A. O. *2287* (5); *540*, *1014*, *1853*, *2289*, *3410*, *5434* (8); —, *2303a*, *2762*, *2793*, *2803a*, *2820*, *3501c* (11).
Garrison, A. W. *37* (8).
Getty, F. — (10).
Gibbons, W. P. *117* (12).
Gilbert, H. C. *875* (7); *877* (9); *874* (10).
Gilkey, H. M. *59* (10).
Goldman, E. A. *176* (11).
Goodding, L. N. —, *2120* (5); *527*, *570*, *1091*, *1627*, *1747* (11).
Gorman, M. W. *443* (7); —, *4124* (9).
Grant, G. B. —, *5216a*, *7072* (7); *1201*, *1974* (7a); *475*, *2004*, *2716*, *3507*, *6172*, *6850*, *9190* (12); *5452* (12a); —, *5144* (14); *1098*, *7068* (16); *4026* (19a).
Grant, J. M. — (6).
Gray, A. — (2); — (4); — (12); — (12a); — (15).
Greene, E. L. — (4); —, *885a* (7); *885* (8); *31*, — (11); — (12); — (14); — (16); — (20).
Gregg, J. *291*, *718* (11).
Gregory, Mrs. — (12).
Griffin, L. H. — (10).
Griffiths, D. *5259* (11).
Griffiths, D. & J. S. Cotton, *534* (8).
Grinnell, F. —, *86*, *87* (12).
Gross, C. A. — (14).
Haley, G. — (7).
Hall, E. *71*, in part (7); *71*, in part (10); *71*, in part (14).
Hall, E. & J. P. Harbour, *85* (5); *18* (11).
Hall, G. R. — (14).
Hall, H. M. *8688*, *9586*, *12136* (7); —, *468*, *674*, *739*, *3196*, *4852*, *6503* (12); *1325*, *11809* (13); *8732*, *8758* (16); *4856* (20).
Hall, H. M. & H. D. Babcock, *4272* (7); *5176*, *5208*, *5434* (7a).
Hall, H. M. & H. P. Chandler, *166* (13); *4772* (16).
Hall, H. M. & M. F. Essig *242* (*10163*) (14).
Hall, H. M. & G. R. *8362*, *8372a*, *8372b*, *8404*, *8481* (7a).
Hammond, E. W. *59* (14).
Hannibal, E. — (3).
Hansen, G. *1671* (3); —, *507*, *508* (4); *505* (7); *241* (11); —, *506* (13); —, *78* (14); *1954* (16).
Hardy, Mrs. M. M. —, (16).
Harper, S. A. & E. T. — (11).
Harrison, G. J. *4861* (11).
Hartweg, T. *1668* (*267*) (1); *1667* (2); *1669* (4); *1666* (12).
Harwood, R. D. & Munz, P. A. *7166* (12).
Hasse, H. E. — (11a); —, *22* (12).
Hatch, D. W. — (9).
Hawver, E. P. — (1).
Hawthorne, J. C. & F. E. Blaisdell, F. E. — (7).
Hayden, F. V. — (11).
Head, A. — (7); — (16).
Heap, J. — (12).
Heckner, J. H. — (7).
Hedgcock, G. G. — (5).
Heermann, A. L. — (11a).
Heller, A. A. *11336* (1); *10751* in part, *11871*, *13937*, *14362* (2); *10751* in part, *11225*, *11381* (3); —, *11298*, *12675*, *13198*, *13934*, *14366* (4); *6047*, *6898*, *9781*, *11645*, *12474*, *14446*, *14647*, *14650* (7); *391*, *10172* (8); *9016* (11); —, *6567*, *7830* (12); *7876*, *7987*, *8105*, *11898*, *12423*, *12744*, *13189* (14); *11879* (15); *7047*, *11656* (16); *9716* (17).
Heller, A. A. & H. E. Brown, *5412*, *5414*, *5452* (1); *5557* (2); *5212* (4); *5227*, *5235* (12); *5496*, *11879* (15).
Heller, A. A. & E. G. *3260* (8).
Heller, A. A. & P. B. Kennedy, *8669* (7).
Henderson, L. F. *1413*, *11360* (6); —, *151*, *7234* *7235* (7); —, *2433*, *2436*, *2437*, *3106*, *5402*, *5631*, *8856*, *8857*, *8858*, *8862* (8); —, *12*, *13*, *24*, *25*, *150*, *11356* (9); —, *27*, *149*, *5998*, *7233*, *10149*, *11357* (14).
Henry, J. K. — (6).
Henshaw, H. W. *121* (12).

Hickman, J. B. — (19).
Hill, E. K. — (4).
Hillman, F. H. — (7).
Hitchcock, A. E. *274* (7); —, *696, 981, 1356½* (11); *370* (16); *549* (17).
Hitchcock, A. S. — (7).
Holder, W. *2537* (12).
Hollick, A. — (1); — (4).
Hooker, J. D. & A. Gray — (16).
Hopping, R. *177* (13).
Horner, R. M. *106, 106B, 115* (8).
House, H. D. *4835* (14).
Howard, J. R. — (7).
Howell, J. T. *2365* (3).
Howell, T. (J.), *734* (6); *606, 1100* in part (7); —, *732, 735, 1100* in part, *1101* (8a); —, *614, 1492* (9); —, *680* (10); —, *603, 733* (14).
Hoyt, J. W. *71* (12).
Hubby, F. W. *28, 67* (12); *8* (12a).
Hull, W. A. *428* (8).
Hunt, Mrs. Clara, — (1).
Jackson, B. R. — (1).
Jaeger, E. C. —, *186* (12).
Jardine, J. T. *310* (8).
Jepson, W. L. — (1); *1174* (3); — (7); — (12).
Jessel, M. S. — (13).
Johnson, O. B. *243* (7).
Johnston, I. M. *1127* (11a); —, *5428, 5441* (12).
Jones, A. J. — (5).
Jones, H. — (8).
Jones, M. E. — (1); — (3); — (4); —, *679, 2139, 6039f* (5); —, *2433* (7); — (7a); —, *5597, 6207, 6208* (8); —, *2182, 3993, 5976b, 5627a, 5983a* (11); — (11b); —, *3157* (12); *6209* (13); — (14); —, *2556* (16); — (17); — (18).
Jones, V. — (7).
Jones, W. W. *133* (4); — (8); *412* (11); *131* (12); *130* (14).
Keck, D. & McCully, *132* (12).
Kelley, D. — (12).
Kellogg, A. & W. G. W. Harford, *111* (1); *110* in part (2); *110* in part (7); *109* (9); *108* (12); —, *106* (20).
Kellogg, W. — (11a); — (12).
Kelly, Mrs. G. Earle — (1).
Kennedy, P. B. *1420* (7); *435, 564, 837, 4395, 4529* (8); *673, 811, 4126* (11).
Kennedy, P. B. & S. B. Doten, *109, 411* (7).
Keyes, E. — (7).
Kildale, D. K. *1188* (7); *803, 1603, 3727* (12); *2280* (14); —, *1837, 3628* (20).
Kincaid, T. — (9).
King, A. M. — (1); — (7); — (12).
Kramer, A. H. — (7).
Krautter, *62* (3).
Lamb, F. H. *1218* (6).
Lathrop, L. M. — (7).
Lawrence, W. E. *818* (8); *1719* (10).
Leach, Mr. & Mrs. J. R. *2422* (14); *2421* (20).
Leeds, B. F. — (1).
Leiberg, J. B. *483, 2657* (7); —, *586, 1140, 2300* (8); *5843* (11); *3248* (12); *4098* (14); *5061, 5284* (16).
Leidy, J. — (8).
Lemmon, J. G. *2646* (11).
Lemmon, Mr. & Mrs. J. G. — (11).
Leonard, F. E. — (11).
Little, E. E. & E. M. Stanton, — (*Pammel 168*) (11).
Lorraine, L. — (7).
Luedinghaus, E. — (9).
Lunell, J. —, *5516* (9).
Lyall, D. — (6).
Lyon, W. T. — (11a).
Macbride, J. F. *165, 412, 1639* (8).
Macbride, J. F. & E. B. Payson, *3807* (8).
McDermott, Mrs. L. — (17).
MacDougal, D. T. *248* (11).
McGregor, E. A. —, *939* (12).
Mackenzie, K. K. *101* (5).
McKeever, H. G. *31* (12).
McLean, T. R. — (12).
Mackie, W. W. — (7).
Macoun, J. —, *53* (6).
McMurphy, J. *160, 836* (1); *161* (20).
Marsh, H. *7739* (5).
Marsh, C. D. *12330* (8).
Marshall, C. C. — (1); — (20).
Mason, H. L. *79* (12).
Mearns, E. A. *72, 265* (11); *3363* (12).
Meehan, T. — (6); — (11); — (12).

Merriam, C. H. — (1).
Merrill, Rev. Dr. — (3).
Metcalfe, O. B. *366*, *1091* (11).
Michener, Miss, — (7).
Michener, C. A. & F. T. Bioletti, — (1); *1344a ?* (12); *423a* (20).
Miles, L. O. —, *172* (8).
Miller, C. E. —, (12).
Minthorn, M. — (7).
Mosier, C. A. — (6).
Moxley, G. L. *586* (7a).
Mulford, A. I. —, *116* (8); *360*, *436*, *436a* (11).
Mulliken, E. *35*, (12); *109* (14).
Munz, P. A. *9866* (1); *3186* (5); *1555* (7a); *4516* (11a); *2144*, *3889*, *6975*, *7166*, *8272*, *8360*, *9233*, *9501*, *9777*, *9778*, *10836* (12); *10271*, *10327* (12a); *7349*, *10572* (13); *11091* (16); *5654*, *10600* (18); *6339* (19a).
Munz, P. A. & I. M. Johnston *5428*, *5441* (12); *8660* (19a).
Murdoch, J. Jr. *4756* (11).
Murdoch, J. M. *2512 2573* (13).
Nelson, A. *7967*, *1489*, (5); *4101* (8); *9069*, *1463* (11).
Nelson, A. & J. F. Macbride, *412*, *1204*, *2104* (8); *1386* (11).
Nelson, E. *651* (5); *4892* (11).
Nelson, E. W. *4543*, *4823*, *6044* (11).
Nelson, J. C. *1296* (5); *2646* (6); *650*, *1294*, *2693*, *3155*, *3843*, *4356*, *4368* (7); *584*, *585*, *658*, *1302*, *3651* (9); *2122*, *3612*, *3640* (10); *1360*, *2678* (14).
Nevin, J. C. *939* (4); —, *254* (12); — (14).
Newberry, J. S. — (2); — (5); — (11).
Newcomer, E. T. — (7).
Newell, G. — (12).
Norton, M. E. — (12).
Norville, Mrs. H. O. — (11).
Nuttall, T. — (9); — (12); — (12a).
Nutting, F. P. — (1).
Oliver, J. C. — (11a).
Orcutt, C. R. —, *305* (12).
Osterhout, G. E. —, *1334* (5); — (11).
Owens, C. E. — (7).
Palmer, E. —, *62* (5); *2532* (7); *203* (7a); *2532* (8); —, *61*, *64*, *117*, *132*, *310* (11); *24* (12); *2519* (14).
Palmer, E. & E. Coues, —, *221* (11).
Pammel, L. H. & R. E. Blackwood, *4111* (8).
Parish, S. B. —, *478*, *1747*, *1804*, *1956*, *2080*, *2199*, *3639*, *3640*, *4687*, *4854*, *9823* (11a); —, *2067*, *2198*, *3640*, *6957*, *11783* (12); *10941* (13); —, *1805*, *2343*, *3172*, *3783* (*3753*), *10876* (18); *3786*, *3826* (19a).
Parish, W. F. & S. B. *1747* (11a).
Parry, C. C. — (1); — (2); — (4); *23*, *85* (*1862*), *429* (5); — (7); —, *24*, *430* (11); — (12); — (16).
Parsons, M. E. — (12).
Patterson, J. R. *49* (7).
Patterson & Wiltz — (12).
Payson, E. B. *138*, *192* (5).
Pease, T. C. — (12).
Pease, Mrs. T. C. — (12).
Pearson, G. A. *279* (11).
Peck, M. E. *6857*, *13420*, (6); *13224*, *6846*, *6848*, *6861*, *6863*, *6864*, *6869*, *6870*, *6871*, *6874*, *6875*, *8029*, *9545*, *10351*, *14314*, *15205*, *15205a*, *15297*, *15404*, *15406*, *15443* (7); *1415*, *6860*, *9331*, *13308*, *15128*, *15408* (8); *6851*, *6867*, *6868* (8a); *6855*, *6856*, *6862*, *6872*, *6874*, *6873* (9); *6866*, *6877* (10); *9068*, *14669* (12); *6878*, *6853*, *6846* (14).
Peckham — (12).
Peebles, R. H. & G. J. Harrison, *4192* (11).
Peebles, R. H., G. J. Harrison, & T. H. Kearney, *2610*, *4314* (11).
Peirson, F. W. *6107* (7); *6867* (8); *2056* (12); —, *2251* (19a); *3774* (20).
Pendleton, R. A. — (7); — (13); — (16).
Pendleton, R. L. *912* (1).
Phelps, K. E. — (9).
Philips, S. — (3).
Pierce, W. M. — (12); — (18).
Piper, C. V. — (1); *723*, *4915* (6); —, *1644*, *1645*, *2396* (8); *6171* (14); — (20).
Pope, A. S. — (6).
Prescott, H. S. — (14).
Price, W. W. — (1); — (14).
Pruett, H. *67* (11a).
Purdy, C. — (12).

Purpus, C. A. *109* (*1090* or *1091*), *4056* (1); *230, 243, 6697* (*6692 ?*) (5); — (7); *5184* (7a).
Randall, A. D. —, *13, 156, 196, 303, 430* (12).
Rattan, V. — (1); — (2); —, *21* (4); — (7); — (12); — (14); — (20).
Read, A. D. *17* (5).
Redfield, J. N. *41* (7); *40* (16).
Reed, F. M. *1351* (12); — (18); *2755* (19a).
Reinoehl, D. — (14).
Reynolds, L. *8988* (9).
Rich, W. H. — (12).
Rixford, G. P. — (4).
Robinson & Crocker — (12).
Rose, J. P. *1713* (8).
Ross — (12).
Rothrock, J. T. *14* (12).
Rusby, H. H. *47* (11).
Rutter, C. *123* (1); — (12).
Rydberg, P. A. *6169* (8).
Rydberg, P. A. & E. C. Carlton, *7486, 7610* (5).
Rydberg, P. A. & A. O. Garrett, *9528* (5); *9211, 9680* (11).
Samuels, E. *29* (1); *31* (12).
Sandberg, J. H. — (8).
Sandberg, J. H., D. T. MacDougal & A. A. Heller — (8).
Sandberg, J. H. & J. B. Leiberg, *586* (8).
Sanford, H. — (12).
Sanford, J. A. — *349* (1); *419* (7); — (8); *426* (16).
Schmitt, W. F. — (12).
Schoenfeldt, L. *3455, 3575* (12).
Schulz, E. D. *289* (5).
Setchell, W. A. — (12).
Setchell, W. A. & C. C. Dobie, — (14).
St. John, O. — (5).
St. John, Mrs. H. — (11).
Shaw, W. R. *583* (12).
Shaw & Illingsworth, *51* (13); *232* (18).
Shear, C. L. *3638* (5); *5622* (9); *3551, 5136* (11).
Shear, C. L. & E. A. Bessey, *3968, 5305* (5).
Sheldon, C. S. *211* (5); *367* (11).
Sheldon, E. P. *8423* (8); *10872* (9).
Sheldon, J. W. — (12).
Sherwood, W. *831* (14).
Smiley, F. J. *188, 325, 672* (7); *884* (16).
Smith, A. H. — (4).
Smith, B. H. — (4); — (5); — (11); — (12); — (12a); — (14).
Smith, C. P. *1876* (5); *1742, 1901* (8).
Smith, L. E. —, *383* (7); *243* (14).
Smith, L. S. *1842* (14).
Smith, R. J. *11* (12).
Snow, F. H. — (5).
Sonne, C. F. — (3); *342* (7); *1428* (12); —, *42, 63* (16).
Spalding, Rev. Mr. — (8).
Spencer, H. —, *2* (10).
Spencer, M. F. —, *146, 2016* (12).
Spiegelberg, C. H. —, *644* (6).
Standley, P. C. *4077, 6588, 14062,* (5); *4966, 6587, 8242, 13872* (11).
Standley, P. C. & H. C. Bollman, *10969* (5); *11040* (11).
Stanford, E. E. *971* (2); *219, 220, 1005* (4); *416, 1083* (14).
Steinbeck, W. P. — (2); — (3); — (16).
Stevenson, E. *119* (8).
Steward, A. N. *173* (9).
Stinchfield, R. *268* (12).
Stokes, S. G. — (8); — (12).
Street, L. — (12).
Sturgis, W. C. — (5); — (11).
Suksdorf, W. N. —, *2446, 2447, 2448, 2449* (8); *1877, 2216* (9); *182* (12a).
Summers, R. W. —, *102* (12).
Sutliffe, E. C. (1); — (7); — (16).
Sutliffe, Mrs. E. C. — (3); — (7); — (19); — (20).
Thompson, C. H. — (12).
Thompson, J. W. *582* (9); *2035, 4389, 4446, 4507, 4584* (14).
Thurber, G. *334, 340, 1664* (11); *334* (11a); *559* (12).
Tidestrom, I. *10391, 10441* (7); — (12); *10562, 10569, 10571* (17).
Torrey, J. *54* (16).
Toumey, J. W. *80* (11).
Townsend, C. H. T. & C. M. Barber, *55* (11).
Tracy, J. P. *1576, 4466, 5539* (1); *5645* (3); *1648* (4); *2288, 2351, 2578, 4831, 5253, 5344, 5394* (7); *1363, 2193, 2194, 3595, 3596, 3597, 3669* (12); *2813,*

3349, 3598, 5713, 7659 (14); *3141, 3010, 3716, 4964* (20).
Tracy J. P. & E. B. Babcock, *3595, 3596, 3597* (12); *3598* (14).
Trelease, W. — (11).
Tweedy, F. *134, 4569* (5); *554, 4570* (11).
Van Dyke, Mrs. E. C. — (7); — (11a); — (12); — (18).
Vasey, G. R. —, *89* (5); — (7); *223* (8); — (11); — (12); — (20).
Vesey, L. J. X. de, *15* in part (11a).
Walker, E. P. *323* (5); *515* (11).
Walker, H. A. *312* (1); *83* (12); *1388* (16).
Wallace — (12).
Walls, E. P. & C. E. Owens — (9).
Watson, S. *194* (5).
Weston, E. R. *167* (7a).
Whited, K. *252, 3099* (7); *486, 2559* (8).
Wiggins, I. L. *1961, 2075* (12).
Wight, W. F. *102* (12).
Wilcox, T. E. — (8).
Wilder, E. M. — (12).
Wilkes Exp. *206* (6).
Williams, T. A. — (8).
Williamson, C. S. — (7); — (12).
Williamson, W. J. *12* (4).
Wislizenus, F. *841* (5); *915* (12).
Wolf, J. & J. T. Rothrock, *14* (11).
Woodhouse, S. W. — (11).
Woods, C. N. *335, 2621* (8).
Woodson, R. E. Jr., *1814* (5).
Wooton, E. O. — (5); —, *192, 2671* (11).
Wright, C. *39, 880* (11).
Wright, W. F. *102* (12).
Wynd, F. L. *1640* (7).
Yates, L. D. — (10).
Yates, L. G. — (12a).
Zuck, M. — (11).

Index to Species

New subgenera, sections, species, varieties and combinations are printed in **bold face** type; synonyms in *italics;* and previously published names in ordinary type.

Page
Adansonia 128
Althaea 118, 125
Annuae 127, 129, 134, 138
Bombacaceae 128
Callirhoë 125
spicata 159, 165
Eumalveae 125
Eusidalcea ... 127, 129, 130, 134, 138, 212
Hesperalcea . 120, 122, 123, 124, 127, 128, 129, 214, 217
§ *Hesperalcea* 118, 214, 217
Hesperalcea 137, 215
malachroides 128, 215
Lavatera 143
Malva 118, 125, 143
malachroides 215, 217
Malvaceae 121, 124
Malvastralcea 120, 122, 123, 127, 128, 130, 211, 212
Malvastrum 125, 128, 212
confertum 213
spicatum 128

Page
Malveae 124
Nuttallia malvaeflora 188
Perennes .. 127, 129, 130, 134, 151, 212
Sida 117, 125, 197
californica 199
delphinifolia 143, 145, 188, 193, 197
diploscypha 139
heterophylla 173
malvaeflora 175, 176, 177, 179, 188, 196, 197, 198
oregana 168, 173, 174
Sidalcea 117, 118, 119, 120, 124, 125, 127, 136, 145, 197, 217
asplenifolia 175, 177
asprella 121, 130, 132, 179, 201, 205, 206, 209
atacosa 218
atropurpurea 218
californica 199
calycosa 124, 145, 147, 151
campestris 132, 133, 169, 174, 175, 177, 178, 179, 197, 218

Page
candida......................
121, 123, 129, 133, 134, 153, 155
candida var. *tincta*...........153, 157
confinis........122, 132, 179, 181, 185
Covillei...................... 187
crenulata..................179, 185
Cusickii...................... 174
delphinifolia....143, 145, 188, 197, 198
delphinifolia var. *humilis*.....189, 198
diploscypha..................
118, 121, 123, 125, 138, 143
diploscypha var. *minor*.......139, 142
elegans................202, 203, 205
eximia................133, 159, 166
favosa....................200, 201
glaucescens...................
130, 132, 158, 187, 205, 207, 209, 210
Hartwegi..........134, 143, 148, 151
Hartwegi var. *tenella*.........148, 151
Hendersoni..................
121, 122, 133, 157, 158, 174, 209
Hickmani.................... 212
Hickmani..................129, 213
Hickmani var. Parishii...129, 130, 213
hirsuta.....................
123, 124, 125, 143, 145, 151, 197
humilis............188, 196, 197, 198
hydrophila................159, 166
interrupta.................166, 167
malachroides.................
118, 123, 125, 128, 215, 217
malvaeflora............121, 132, 145,
177, 184, 185, 187, 188, 197, 198, 201
malvaeflora..................
156, 157, 168, 179, 184, 187, 197, 198
malvaeflora var. *asprella*......... 202
malvaeflora var. atropurpurea.... 218
malvaeflora var. californica...... 199
malvaeflora var. Listeri......... 218
malvaeflora var. *Oregana* .157, 168, 174
mariana..................... 218
mexicana.................... 218
montana...................207, 209

Page
multifida..................130, 209
"*Murrayana*"................ 159
Nelsoniana............159, 161, 165
neo-mexicana.................
121, 122, 129, 132, 156, 157, 179,
184, 185, 187, 197, 198, 201, 209
neo-mexicana var. **Covillei**...132, 187
neo-mexicana var. *Diehlii*.179, 184, 185
neo-mexicana var. **parviflora**....
132, 186, 188
nervata..................169, 174
nitrophila.................122, 186
nodosa...................... 218
oregana..............132, 133, 158,
168, 174, 175, 177, 185, 197, 198, 209
oregana var. **Cusickii**.......133, 174
Parishii..................... 213
parviflora..........122, 185, 186, 187
parviflora var. *Thurberi*..132, 179, 185
pedata................130, 151, 210
peruviana.................... 218
ranunculacea..............166, 167
reptans...............132, 200, 201
rhizomata......122, 145, 146, 147, 148
robusta..............130, 205, 206
rostrata...............189, 190, 198
scabra...................189, 198
secundiflora..............139, 143
spicata........132, 133, 159, 165, 166
spicata var. *pedata*............. 210
spicata var. **ranunculacea**...... 166
spicata var. *reptans*............ 200
sulcata..............145, 147, 148
sylvestris.................175, 177
tenella...................148, 151
triloba...................... 218
valida...............159, 165, 166
virgata...............132, 174, 178
vitifolia..................215, 217
Sidalcia...................... 145
Sphaeralcea.................125, 213
pedatifida.................. 218

Explanation of Plate

PLATE 5

Fig. 1. Perfect flower of *S. malvaeflora* (DC.) Gray. × ⅔.

Fig. 2. Pistillate flower of *S. malvaeflora* (DC.) Gray. × ⅔.

Fig. 3. Longitudinal section of the stamineal column of *S. candida* Gray, showing the outer and inner series of phalanges. × 3.

Fig. 4. Stamineal column of *S. diploscypha* (Torr. & Gray) Gray, typical of the section *Annuae*. × 3.

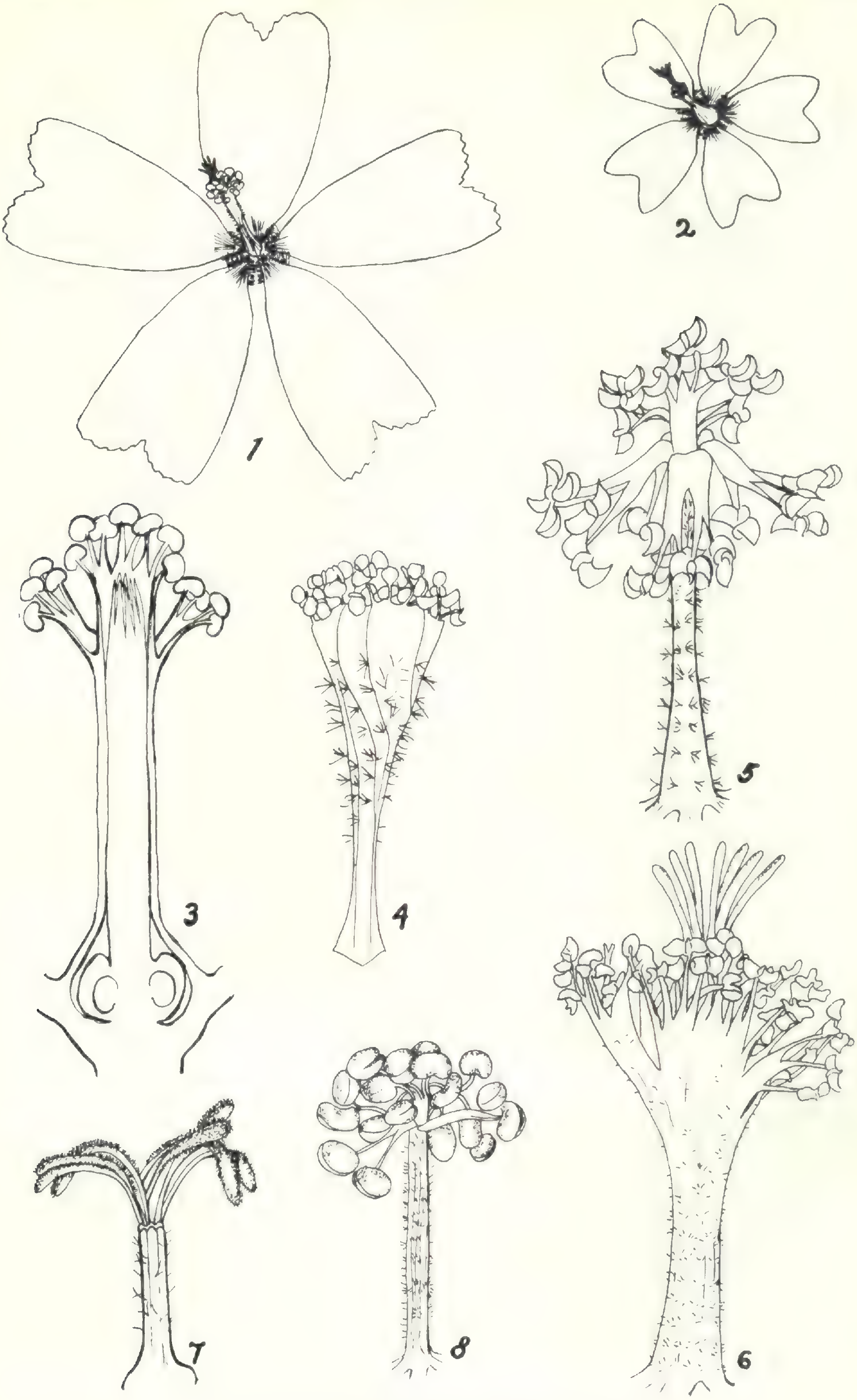
Fig. 5. Stamineal column of *S. candida* Gray, typical of the section *Perennes*. × 3.

Fig. 6. Stamineal column of *S. Hickmani* var. *Parishii* Rob., typical of the subgenus *Malvastralcea*. × 3.

Fig. 7. Stamineal column of the pistillate flower of *S. malachroides* (H. & A.) Gray of the subgenus *Hesperalcea*. × 3.

Fig. 8. Stamineal column of the perfect flower of *S. malachroides* (H. & A.) Gray of the subgenus *Hesperalcea*. × 3.

Del. C. K. Allen



ROUSH—MONOGRAPH OF SIDALCEA

Explanation of Plate

PLATE 6

Photomicrographs of the dorsal and lateral surfaces of carpels of *Sidalcea*, illustrating the various types of markings in the subgenera and section. Magnification approximately 10 diameters.

Subgenus *Eusidalcea*—Section *Annuae.*

Fig. 1. *S. hirsuta* Gray.
Fig. 2. *S. Hartwegi* Gray.
Fig. 3. *S. calycosa* M. E. Jones (entire fruit, viewed from above).
Fig. 4. *S. calycosa* M. E. Jones.

Subgenus *Eusidalcea*—Section *Perennes.*

Fig. 5. *S. spicata* (Regel) Greene.
Fig. 6. *S. oregana* (Nutt.) Gray.

Subgenus *Malvastralcea.*

Fig. 7. *S. Hickmani* var. *Parishii* Rob.

Subgenus *Hesperalcea.*

Fig. 8. *S. malachroides* (H. & A.) Gray.

ROUSH—MONOGRAPH OF SIDALCEA

Explanation of Plate

PLATE 7

Sidalcea diploscypha (Torr. & Gray) Gray, from *Heller & Brown No. 5412*, in the Herbarium of Leland Stanford, Jr. University, typical of the subgenus *Eusidalcea* section *Annuae*.

ROUSH—MONOGRAPH OF SIDALCEA

Explanation of Plate

PLATE 8

Fig. 1. *Sidalcea candida* Gray, from *Palmer No. 62* in the Missouri Botanical Garden Herbarium, showing usual variation of leaves in the subgenus *Eusidalcea* section *Perennes*.

Fig. 2. *Sidalcea campestris* Greene, from the cotype, *T. J. Howell No. 614* in the Gray Herbarium of Harvard University.

1

2

ROUSH—MONOGRAPH OF SIDALCEA

Explanation of Plate

PLATE 9

Fig. 1. *Sidalcea oregana* (Nutt.) Gray, from *Greene No. 885* in the Missouri Botanical Garden Herbarium, typical of the more harshly puberulent form.

Fig. 2. *Sidalcea oregana* (Nutt.) Gray, from type specimen of *S. nervata* A. Nelson, *A. Nelson No. 4101* in the Rocky Mountain Herbarium, the more eastern and almost glabrous form.

1

2

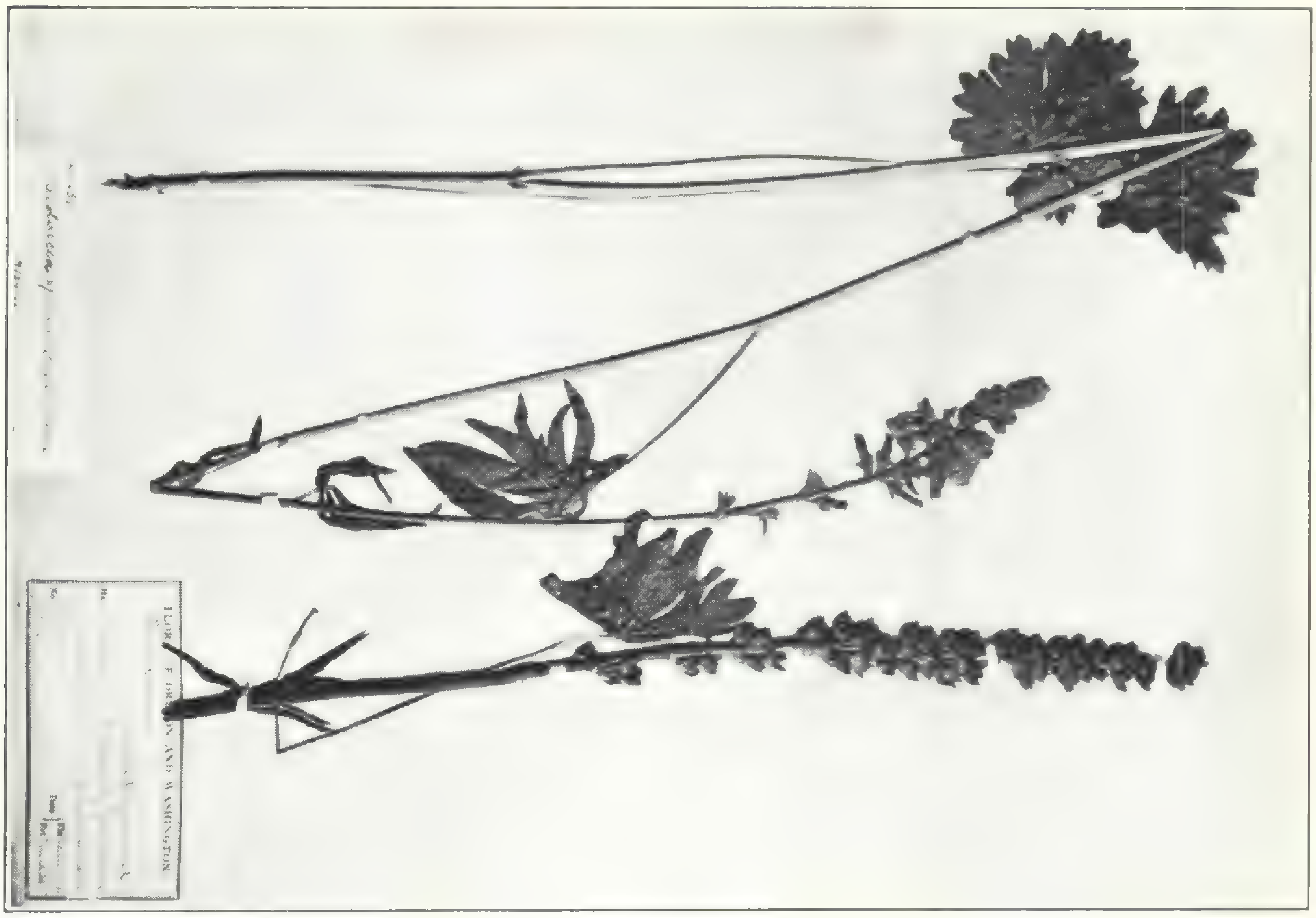
ROUSH—MONOGRAPH OF SIDALCEA

Explanation of Plate

PLATE 10

Fig. 1. *Sidalcea spicata* (Regel) Greene, from *Henderson No. 151* in the Herbarium of Oregon University, typical of the more hirsute form.

Fig. 2. *Sidalcea spicata* (Regel) Greene, from *Cusick No. 2053* in the Herbarium of Oregon University, the stellate-pubescent form.



1

2

ROUSH—MONOGRAPH OF SIDALCEA

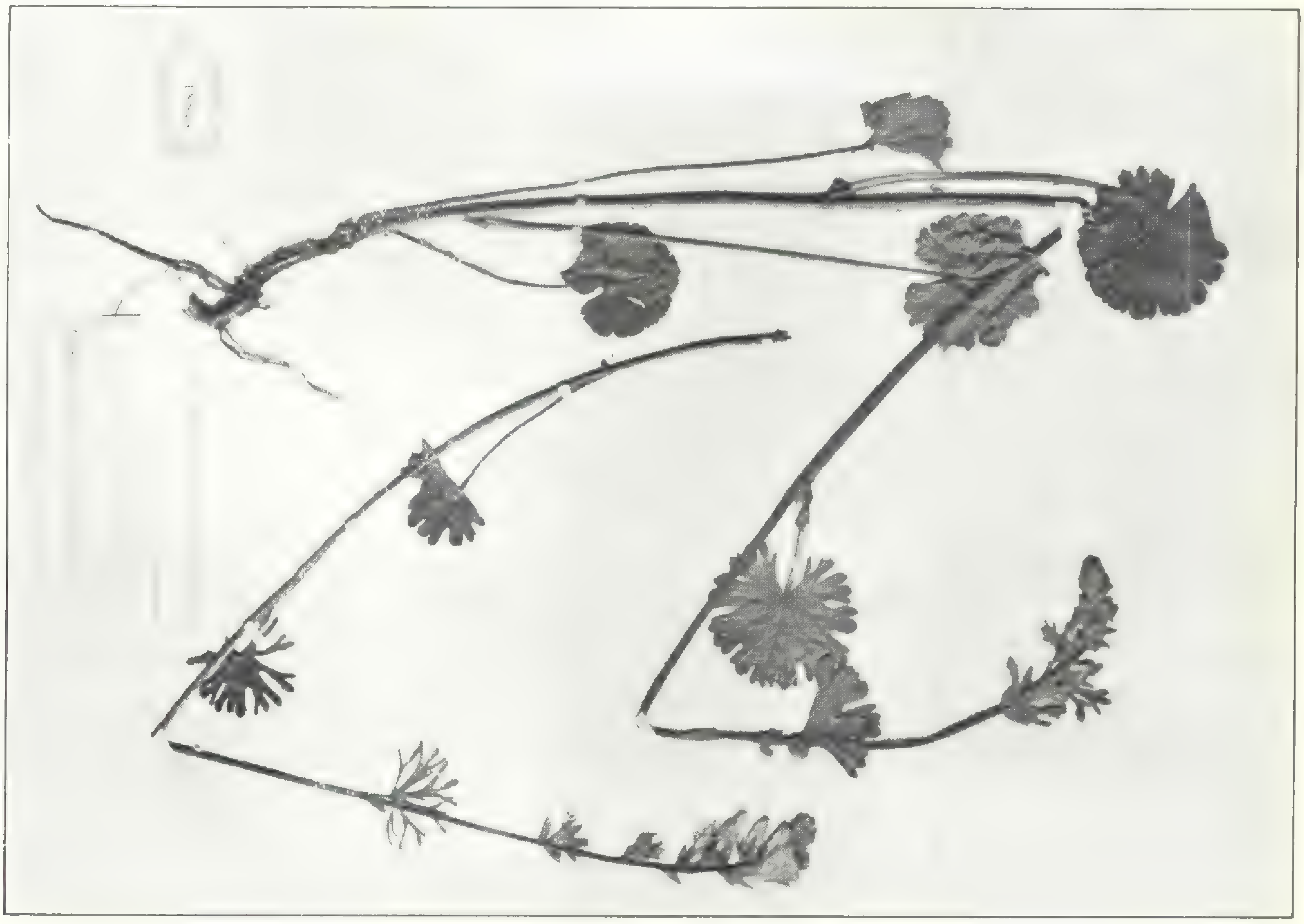
Explanation of Plate

PLATE 11

Fig. 1. *Sidalcea malvaeflora* (DC.) Gray, from authentic material, *Hartweg No. 1666*, *Fremont*, and *Bigelow*, in the Gray Herbarium of Harvard University, typical of the low decumbent form.

Fig. 2. *Sidalcea malvaeflora* (DC.) Gray, from *Greene* in the Herbarium of the University of California No. 18856, typical of the more erect, robust form.

1



2

ROUSH—MONOGRAPH OF SIDALCEA

Explanation of Plate

PLATE 12

Fig. 1. *Sidalcea multifida* Greene, from authentic material, *A. A. Heller No. 9716* in the United States National Herbarium, showing the caespitose habit of the section *Perennes*.

Fig. 2. *Sidalcea pedata* Gray, from type specimen, *S. B. Parish No. 1805* in the Gray Herbarium of Harvard University, showing the subscapiform habit.

1

2

ROUSH—MONOGRAPH OF SIDALCEA

Explanation of Plate

PLATE 13

Fig. 1. *Sidalcea Hickmani* var. *Parishii* Rob., from the type specimen, *S. B. Parish No. 3786* in the Gray Herbarium of Harvard University, illustrating the subgenus *Malvastralcea*.

Fig. 2. *Sidalcea malachroides* (H. & A.) Gray, from *Davy No. 5482* in the Herbarium of the University of California, illustrating the subgenus *Hesperalcea*.

1

ROUSH—MONOGRAPH OF SIDALCEA

2

A REVISION OF THE GENUS FRASERA[1]

HAMILTON H. CARD

Formerly Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany of Washington University

Introduction

The present study was undertaken to determine the status of the genus *Frasera*. In recent years it has received various treatments in the numerous local manuals and floras; certain authors have considered it a portion of the more polymorphic and widespread genus *Swertia*, others have regarded it as a distinct generic unit, whereas still others have segregated it into several smaller genera.

Sincere appreciation is due the curators of the herbaria of the University of California, Field Museum of Natural History, Gray Herbarium of Harvard University, and the Los Angeles Museum, for the loan of material necessary in this study. For the use of the excellent library and herbarium of the Missouri Botanical Garden, especial thanks are due the Director, Dr. George T. Moore. The writer desires to express his appreciation to Dr. J. M. Greenman, Curator of the Herbarium of that institution, and to Dr. Mildred E. Mathias, Research Assistant, who have so generously given their advice from time to time.

History of the Genus

Walter[2] described the genus *Frasera* in 1788, naming it in honor of John Fraser, a noted plant collector of the eighteenth century. A single species, *Frasera caroliniensis*, was assigned to the new genus. Fifteen years later Michaux[3] recognized the genus, renaming the species *F. Walteri*. Pursh[4] in 1814 recognized

[1] An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

[2] Walt. Fl. Carol. 87. 1788.

[3] Michx. Fl. Bor. Am. **1**: 96. 1803.

[4] Pursh, Fl. Am. Sept. **1**: 101. 1814.

Issued June 30, 1931.

F. Walteri, indicating its occurrence "In swamps of Lower Carolina and on the borders of lakes in Pennsylvania and New York."

In 1828 Rafinesque[5] included the genus in his 'Medical Flora,' listing but a single species, *F. verticillata*, which he admitted to be identical with *F. caroliniensis*. At the same time Rafinesque suggested the name *Mesadenia* as being more appropriate than *Frasera*. Four varieties of *F. verticillata* were also proposed in the 'Medical Flora.'

In 1839 two closely related species, *F. nitida* and *F. albicaulis*, were added to the genus. The one, *F. nitida*, was described by Bentham[6] from material collected by Hartweg "in montibus Sacramento," California, and the other, *F. albicaulis*, by Grisebach,[7] based on specimens collected by Douglas in the vicinity of Spokane, Washington, and Kettle Falls, British Columbia.

Grisebach[8] revised the Gentianaceae for Hooker's 'Flora Boreali-Americana' in 1840, publishing another of Douglas's manuscript names as *F. speciosa*. In 1844, in de Candolle's 'Prodromus' Grisebach[9] recognized the genus *Frasera* and included all the species previously known.

In 1851 Hooker[10] published *F. thyrsiflora*. During the later years of the same decade Dr. John Torrey added two species to the genus, namely, *F. paniculata*[11] and *F. Parryi*.[12] Kellogg[13] in 1862 proposed the new genus *Tesseranthium*, designating the type species as *T. radiatum*. It has since been shown that *T. radiatum* Kellogg is conspecific with *Frasera speciosa* Douglas.

Since 1871 approximately fifteen new species and varieties have been described in the genus but no recent comprehensive survey of the group has been made. Treatments of the genus have appeared in the various local manuals and floras; certain workers[14] have segregated the genus into several closely allied genera,

[5] Raf. Med. Fl. **1**: 196. 1828.
[6] Benth. Pl. Hartw. 322. 1839.
[7] Griseb. Gen. et Sp. Gent. 330. 1839.
[8] Griseb. in Hook. Fl. Bor.-Am. **2**: 65–67. 1840.
[9] Griseb. in DC. Prodr. **9**: 131. 1844.
[10] Hook. Kew. Jour. **3**: 288. 1851.
[11] Torr. in Pacif. R. R. Rept. **4**: 126. 1856.
[12] Torr. Bot. Mex. Bound. Surv. 156. 1859.
[13] Kell. in Proc. Calif. Acad. Sci. **2**: 142. 1862.
[14] Rydb. Fl. Rocky Mts. 664–666. 1917, and ed. 2, 664–666. 1922.

namely, *Frasera, Tessaranthium* and *Leucocraspedum;* on the other hand, Gilg,[15] in Engler and Prantl, 'Die Natürlichen Pflanzenfamilien,' and Jepson[16] in his recent 'Manual' have merged the genus *Frasera* and its segregates with *Swertia.*

General Morphology

Roots.—The prevailing root type in the genus *Frasera* is the tap-root. In the majority of species this tap-root grades directly into the stem, but in some of the western species, particularly *F. nitida, F. montana,* and *F. neglecta,* the root grades into a branching underground rhizome before being transformed into the aërial stem. The former group is therefore composed of biennial or short-lived species, whereas the latter is composed of perennials. Occasionally the biennial species may persist for more than two years, but that phenomenon is evidently never accompanied by the formation of a true rhizome as in the strictly perennial species.

The tap-root may be greatly thickened and fleshy, as in the species *F. caroliniensis, F. fastigiata,* and *F. speciosa,* or relatively slender and fibrous, as in *F. paniculata.*

Stems.—An herbaceous aërial stem terminates the unbranched crown of the root in the biennial or short-lived species. In the perennial species, however, the existence of the underground branching rhizome is a striking feature. The aërial stems show but slight variation, all being uniformly simple, erect, terete, and frequently strongly fistulose. The surface may be glabrous, glaucous, or variously pubescent. The height of the stem varies with the species. *Frasera caroliniensis* and *F. speciosa* have the highest stems, frequently reaching two or three meters. The far-western species are less conspicuous and rarely exceed one-half meter in height.

The stems of *F. caroliniensis, F. fastigiata,* and *F. speciosa* are truly foliose, the leaves ascending the stem at regular nodes, and grading into the foliaceous bracts of the inflorescence. In the remaining species, however, the stem may be described as scapose or subscapose, for the foliage is almost entirely limited to a basal

[15] Gilg. in Engl. & Prantl, Nat. Pflanzenfam. 4^2: 87. 1895.
[16] Jepson, Man. Fl. Pl. Calif. 766. 1925.

rosette, the stem proper being naked or only bearing isolated and conspicuously reduced leaves at irregular intervals.

Leaves.—The simple, entire leaves are opposite or in whorls of three to six, disposed on an upright stem or forming a basal rosette, and are either sessile or petiolate. They vary in outline from ovate to almost linear. The margins of the leaves in certain species, such as *F. albomarginata*, often become conspicuously whitened and minutely tuberculate or papillate. While some of the plants of this group are glabrous throughout, certain species have a scaberulent tomentum. The texture of the leaves in the fresh state is with few exceptions somewhat fleshy; the leaves of dried pressed specimens, however, are more or less membranous. The venation of the leaves of the various species is characteristic; in *F. caroliniensis* and *F. fastigiata* a conspicuous midrib is developed, presenting a penninerved appearance, whereas in certain other species the veins are more or less parallel.

Inflorescence.—The mode of inflorescence is cymose and among the different species assumes characteristic modifications which have been found to be of taxonomic value. Text-figure 1 shows a diagram of the various types of inflorescence occurring in the genus. Each diagram represents a single axillary unit of inflorescence, b-b′ representing the subtending leaves. In fig. 5 the condition of the leaf, b-b′, subtending a single, much-branched peduncle, is here interpreted as a primitive inflorescence. Figures 4, 3, 2, and 1 show a progressive sequence in inflorescence specialization which culminates in the advanced type[17] illustrated in fig. 1, in which several relatively disorganized peduncles and solitary flowers are borne in the axil of the subtending leaf (b-b′). The development of the advanced types is probably due to a successive shortening or a submergence of the primary axes of the simple axillary inflorescences until finally only the tips, or pedicels, remain distinct, giving the inflorescence a fasciculate appearance. The single axillary inflorescence type is exemplified by *F. paniculata* although the main axis is cymose. In *F. Parryi*, however, the main axis is unbranched, and the flowers are borne in a raceme.

[17] Parkin, J. The evolution of the inflorescence. Jour. Linn. Soc. Bot. **42:** 511–563. 1914.

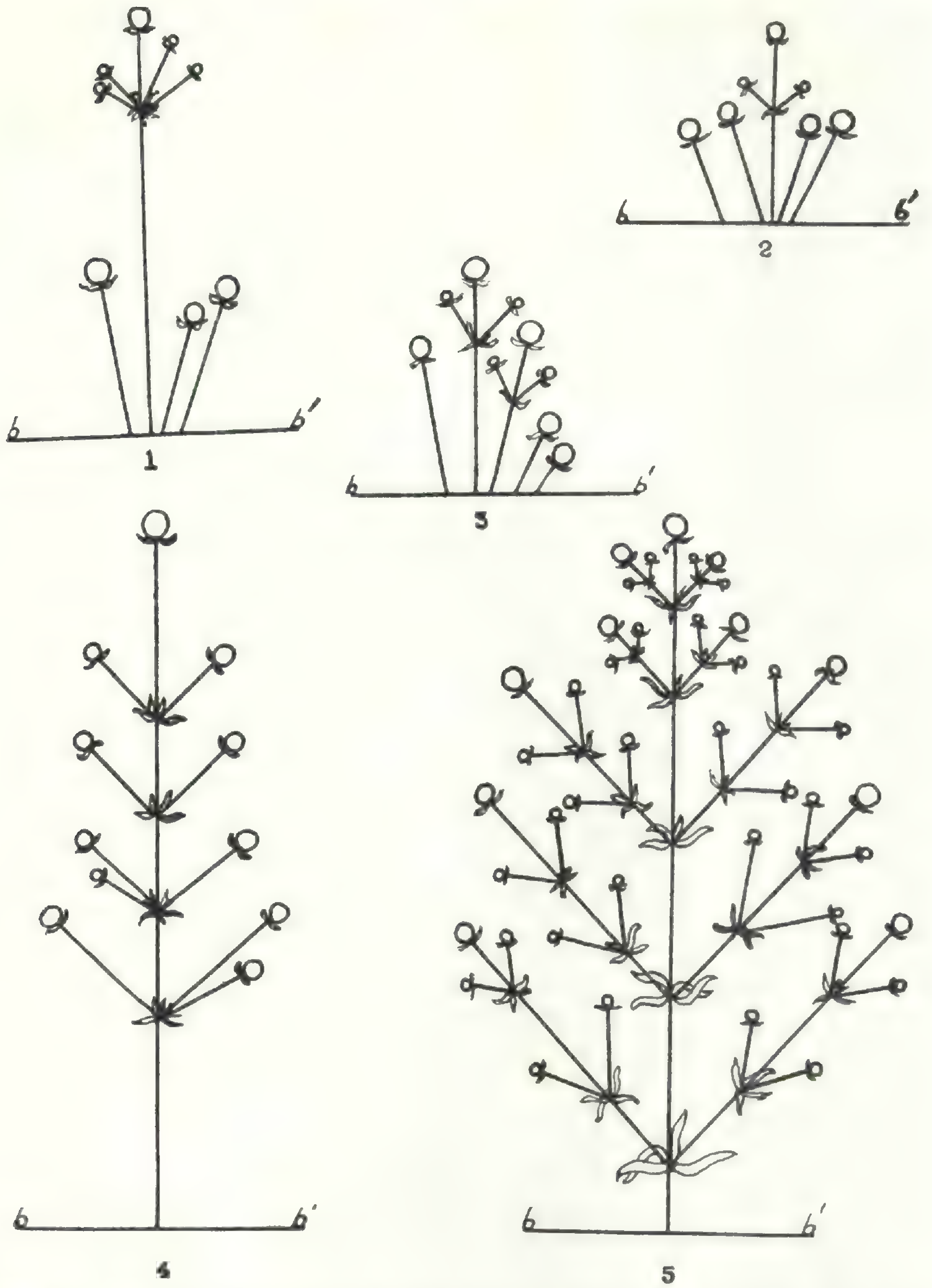


Fig. 1. Diagrams showing the various types of inflorescence within the genus *Frasera:*

1. *F. nitida.*
2. *F. speciosa.*
3. *F. caroliniensis.*
4. *F. Parryi.*
5. *F. albomarginata.*

The condition of the inflorescence of *F. caroliniensis*, *F. fastigiata*, and *F. speciosa* is more advanced than that of the foregoing species. In each, many pedicels, reduced peduncles, and numerous bracts are found in the axil of each leaf. This condition, as has been said before, is believed to be the result of the submergence of a single cyme.

The most specialized type of inflorescence occurs in *F. nitida* and related species. In these species the peduncle is usually obsolete and the leaf subtends several distinct pedicels. The presence of numerous bracts mingled with the pedicels, however, cannot be ignored.

Calyx.—The calyx is gamosepalous and deeply 4-parted, and at the base of the short tube there frequently occur minute filamentous processes known as squamellae. The lobes are usually subulate, but vary from linear to obovate.

Corolla.—The corolla is gamopetalous, deeply 4-parted, and rotate. There is considerable variation in size and shape of the lobes, some being oblong and mucronate, others obovate and acute, and still others oval or broadly oblong. The corolla, moreover, is rather firm in texture, and is usually greenish-white in color with the lobes often profusely blotched with blackish or dark-greenish maculations.

One or two glandular pits are borne on the ventral surface of each lobe. These structures (pl. 14), called foveae, assume bizarre and characteristic shapes, being usually circular, sagittate, oblong, or quadrate, at other times linear with an obcordate apex. The margins of the foveae are usually bordered by a conspicuous ciliation.

In several species, in addition to the foveae and generally contiguous with them, occurs a conspicuous *corona* or crown, which may be either fringed, petaloid, or a combination of both. In other species the crown is lacking, or almost obsolete.

Stamens.—There are four stamens, alternate with the lobes of the corolla. The filaments are inserted at the very base of the obscure tube, are about as long as the corolla, and linear or somewhat dilated at the base. The anthers are two-celled, oblong, versatile, extrorse, and longitudinally dehiscent. The pollen is granular.

Ovary.—The ovary is bicarpellary, unilocular, usually ovate-fusiform, and subsessile; the terminal portion is gradually attenuated into a filiform style. The stigma is two-cleft, the plane of either lobe coinciding with the plane of placentation. The placentae are parietal and binate, and upon each placenta are arranged two to four rows of anatropous ovules.

Fruit.—The fruit is a capsule, enclosed by the persistent perianth. The capsule is usually flattened parallel to the valves, but in some species it is flattened contrary to the valves. The seeds are numerous, ovate or triangular, flat, and in some species variously winged about the margin.

Geographical Distribution

The distribution of the genus *Frasera* is limited to the region of North America lying between 25° and 50° North latitude, which is approximately coincident with the northern and southern boundaries of the United States. The genus occurs in two distinct areas, one in the eastern and southeastern United States, extending as far north as southern Michigan and west to the eastern limit of the great plains region, the other extending from the one hundredth meridian west to the Pacific coast. The former area is occupied by the single species, *F. caroliniensis*, while the remaining species are confined to the latter area, as the accompanying map indicates.

The genus at one time probably had a continuous transcontinental distribution and its present occurrence in two such widely separated areas is presumably the result of isolation following the invasion of the Upper Cretaceous sea which separated the continent into an eastern and western portion.

Although the western species seem to be more abundant at the higher altitudes, yet they are able to maintain themselves in a variety of habitats. The changes in the character of the plants are the results of the various environmental factors, soil, moisture, altitude, etc. *Frasera fastigiata*, for instance, grows in rich, moist valleys, developing thin membranous leaves, whereas the species of the mountainous and desert regions have a decidedly fleshy or coriaceous texture.

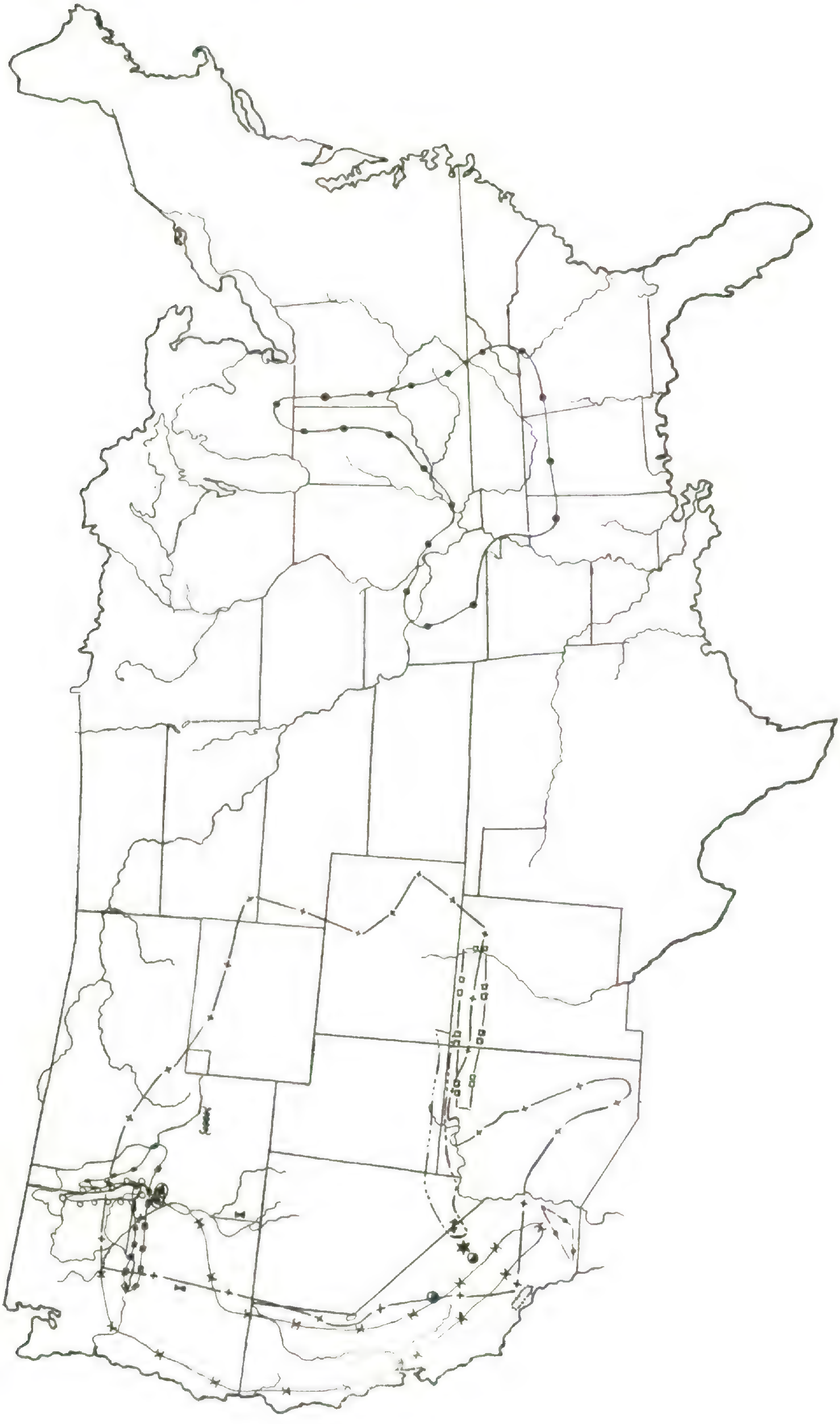


Fig. 2.

Fig. 2. Map showing the distribution of the genus *Frasera* in North America.

F. caroliniensis.
F. fastigiata.
F. nitida var. *Cusickii.*
F. neglecta.
F. albomarginata.
F. speciosa.
F. Parryi.
F. tubulosa.
F. nitida.
F. montana.
F. nitida var. *albicaulis.*
F. coerulea.
F. paniculata.
F. puberulenta.
F. albomarginata var. *induta.*

Phylogeny

The interrelationship among the various species of *Frasera* is so evident that any discussion concerning their phylogeny is problematical.

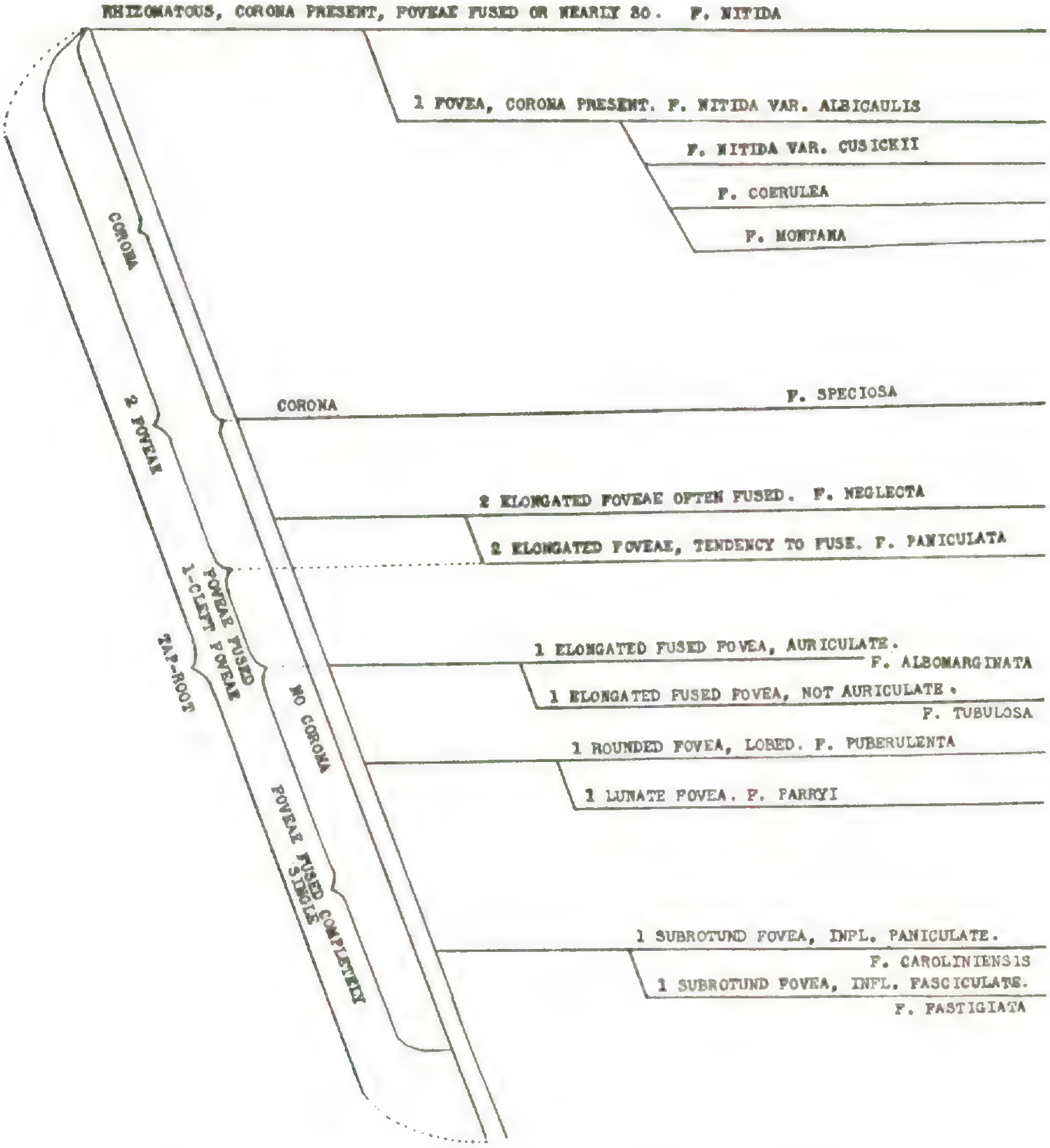


Fig. 3. Diagram showing tendencies toward fusion of the foveae.

The primitive floral condition in the genus may be considered as that represented by such species as *F. speciosa* and *F. nitida,* in which a corona and two foveae are present. The absence of corona and the occurrence of only a single fovea, as in *F. fastigiata,* represent the more advanced type of development.

Among the western species there are two lines of descent, one represented by the coastal species and the other by the more inland forms. The most primitive of the more coastal species is considered to be *F. nitida*, with a corona and two variously fused foveae. *Frasera neglecta*, with two more or less fused foveae, is probably a lateral offshoot from *F. nitida*. The second line of development begins with *F. speciosa*, the most primitive of the species in the genus because of its corona and two distinct

Fig. 4. Diagram showing probable lines of development within the genus *Frasera*.

foveae, as well as the somewhat primitive type of inflorescence in which only partial submergence of the peduncles occurs. *Frasera paniculata* and *F. albomarginata* are the least removed from *F. speciosa*. In the two former species the foveae have become variously fused. A more advanced condition is that represented by *F. Parryi* and *F. puberulenta*, with only a single variously cleft or lobed fovea. *Frasera fastigiata* and *F. caroliniensis* with a single fovea and a more advanced type of inflorescence culminate this line of descent.

These two lines of development within the genus, as illustrated in the accompanying charts (figs. 3 and 4) and distribution map

(fig. 2), are more or less paralleled by the geographical range of the various species.

Medicinal Usage

In the early part of the nineteenth century *Frasera* was variously known as "American Colombo," "Colombo-root," "Columbia," "Indian Lettuce," "Yellow Gentian," "Golden Seal," "Curcuma," "Meadow Pride," "Pyramid," etc.

It is not now recognized in the 'United States Pharmacopoeia,' but one hundred years ago its medicinal properties were considered very great. Relative to its therapeutical effect, Dr. Daniel Drake[18] writes as follows: "The root of Frasera is a pure, powerful, and excellent bitter, destitute of aroma. It may be used in powder, decoction, infusion, and tincture." Further, Rafinesque attributes to it an almost miraculous power: "Emetic and cathartic when fresh, tonic, antiseptic and febrifuge when dry. It has cured a wide spread gangrene of the lower limbs by internal use and external application when bark had failed."[19] Others say that "it is employed in jaundice, scurvy, gout, and is a specific in hydrophobia!"

Abbreviations

The list of abbreviations of herbaria used in the citation of specimens is as follows:

G = Gray Herbarium of Harvard University.
F = Field Museum of Natural History.
C = University of California.
M = Missouri Botanical Garden.
LA = Los Angeles Museum.

Taxonomy

Frasera Walt. Fl. Carol. 87. 1788; Michx. Fl. Bor.-Am. **1**: 96. 1803; Pursh, Fl. Am. Sept. **1**: 101. 1814; Raf. Med. Fl. **1**: 196. 1828; Benth. Pl. Hartw. 322. 1839; Griseb. Gen. et Sp. Gent. 330. 1839; in Hook. Fl. Bor.-Am. **2**: 66. 1840; in DC. Prodr. **9**: 131. 1845; Benth. & Hook. Gen. Pl. **2**: 817. 1876;

[18] Drake in Barton, Veg. Mat. Med. U. S. **2**: 109. 1818.
[19] Raf. Med. Fl. **1**: 199–200. 1828.

Gray, Syn. Fl. N. Am. **2**[1]: 111, 125. 1878, and ed. 2, **2**[1]: 111, 125. 1886; Chapman, Fl. S. U. S., ed. 3. 340. 1897; Howell, Fl. N. W. Am. 447. 1897; Piper in Contr. U. S. Nat. Herb. **11**: 451. 1906; Gray, Man. Bot., ed. 7, 659. 1908; Britt. & Brown, Ill. Fl. **3**: 14. 1913; Small, Fl. S. E. U. S. 931. 1913; Wooton & Standl. in Contr. U. S. Nat. Herb. **19**: 499. 1915; Rydb. Fl. Rocky Mts. 664. 1917, and ed. 2, 664. 1922; Tidestrom in Contr. U. S. Nat. Herb. **25**: 417. 1925; Jepson, Man. Fl. Pl. Calif. 765. 1925.

Mesadenia Raf. Med. Fl. **1**: 198. 1828.

Tesseranthium Kellogg in Proc. Calif. Acad. Sci. **2**: 142. 1862.

Tessaranthium Rydb. Fl. Rocky Mts. 666. 1917, and ed. 2, 666. 1922.

Sweertia L. acc. to O. Ktze. Rev. Gen. **2**: 430. 1891, in part; Gilg in Engl. & Prantl, Nat. Pflanzenfam **4**[2]: 87. 1895, in part.

Leucocraspedum Rydb. Fl. Rocky Mts. 665. 1917, and ed. 2, 665. 1922.

Swertia L. acc. to Jepson, Man. Fl. Pl. Calif. 766. 1925, in part.

Herbaceous caulescent biennials or perennials from a taproot, sometimes forming rhizomes. Stems erect, simple, terete, fistulous, leafy, scapose to subscapose. Leaves opposite or whorled, lanceolate to spatulate, sessile or narrowed at the base into a petiole, membranous or coriaceous, sometimes white-margined, penninerved to subparallel-veined. Inflorescence terminal, flowers disposed in a subcorymbose, thyrsoidal or loosely paniculate cyme. Calyx 4-parted, the lobes deeply cleft, subulate, acute. Corolla rotate, 4-parted nearly to the base; the tube shallow, flat, with or without a conspicuous crown; the lobes convolute in the bud and bearing on the ventral surface one or two more or less fringed glandular foveae. Stamens four, inserted on the corolla tube and alternate with the lobes; filaments linear or somewhat dilated at the base; anthers 2-celled, oblong, versatile, extrorse, longitudinally dehiscent. Ovary bicarpellary, unilocular, the terminal portion gradually attenuate into a filiform style; stigma 2-cleft; placentae parietal, binate, bearing numerous anatropous ovules. Capsule ovate, bivalvate, compressed either parallel or contrary to the valves, 4–20-seeded. Seeds ovate, triangular, flat, pitted, variously winged or rugose. Embryo erect.

Type species: *Frasera caroliniensis* Walt. Fl. Carol. 87. 1788.

KEY TO THE SPECIES

A. Plant not scapose; inflorescence foliaceous-bracteate throughout; leaves not white-margined.
  B. Corolla-lobe bearing a pair of foveae upon its ventral surface; crown conspicuous; capsule flattened contrary to the valves....*1. F. speciosa*
  BB. Corolla-lobe bearing a single fovea upon its ventral surface; crown inconspicuous or lacking; capsule flattened parallel to the valves.
    C. Inflorescence relatively loose, leafy; pedicels exceeding the flowers; corolla-lobes oblong-ovate, 1–2 cm. long; species mostly of the southeastern United States........................*2. F. caroliniensis*
    CC. Inflorescence relatively compact, bracteate; pedicels shorter than the flowers; corolla-lobes oblong-lanceolate, 0.8–1 cm. long; species of the northwestern United States...................*3. F. fastigiata*

AA. Plants scapose to subscapose; inflorescence not foliaceous-bracteate throughout; leaves may or may not be conspicuously white-margined.
  B. Perennials from a branching somewhat woody rhizome; leaves opposite.
    C. Basal leaves lance-attenuate to oblanceolate, 5–20 cm. long.
      D. Plants 3 dm. or more high; flowers several in the axils.
        E. Lower branches of the inflorescence long-pedunculate, 5–10 cm. long; flowers relatively large....................*4. F. neglecta*
        EE. Lower branches of the inflorescence short-pedunculate, 1–1.5 cm. long; flowers relatively small.
          F. Inflorescence about 3 cm. in diameter.............*5. F. montana*
          FF. Inflorescence about 2 cm. in diameter.
            G. Plants glabrous................................*6. F. nitida*
            GG. Plants more or less pubescent......*6a. F. nitida* var. *albicaulis*
      DD. Plants from 1.5–2.5 dm. high; flowers one or two in the axils.
        E. Inflorescence dense....................*6b. F. nitida* var. *Cusickii*
        EE. Inflorescence open................................*7. F. coerulea*
    CC. Basal leaves spatulate, 4–9 cm. long...................*8. F. tubulosa*
  BB. Perennials from a somewhat woody tap-root; leaves opposite.
    C. Inflorescence a paniculate cyme; crown absent; fovea oblong...... ....*9. F. puberulenta*
    CC. Inflorescence a corymbose cyme; crown present; fovea lunate...... ....*10. F. Parryi*
  BBB. Perennials from a somewhat woody tap-root; leaves whorled.
    C. Pedicels 0.5–0.6 cm. long; fovea not two-parted, apical tooth lacking.
      D. Plants glabrous throughout....................*11. F. albomarginata*
      DD. Plants glandular-puberulent throughout...................... ....*11a. F. albomarginata* var. *induta*
    CC. Pedicels 2–4 cm. long; fovea usually deeply 2-parted, with a conspicuous apical tooth................................*12. F. paniculata*

1. F. speciosa Dougl. in Hook. Fl. Bor. Am. **2**: 66. 1840; Wats. Bot. Wheeler Exp. 279. 1871; Gray, Syn. Fl. N. Am. **2**[1]: 125. 1878; Coulter, Man. Bot. Rocky Mt. 246. 1885; Nels.

in Coult. & Nels. Man. Bot. Cent. Rocky Mts. 384. 1909; Wooton & Standl. in Contr. U. S. Nat. Herb. **19**: 500. 1915; Tidestrom in Contr. U. S. Nat. Herb. **25**: 417. 1925; Garrett, Spring Fl. Wasatch Reg. 119. 1927. Pl. 14, fig. 4.

Tesseranthium radiatum Kellogg in Proc. Calif. Acad. Sci. **2**: 142. 1862.

Sweertia radiata (Kellogg) O. Ktze. Rev. Gen. **2**: 430. 1891.

Frasera speciosa Dougl. var. *scabra* Jones, Zoe **4**: 277. 1893; Nels. in Coult. & Nels. Man. Bot. Cent. Rocky Mts. 384. 1909.

F. venosa Greene, Pittonia **4**: 185. 1900; Wooton & Standl. in Contr. U. S. Nat. Herb. **19**: 500. 1915.

F. macrophylla Greene in Pittonia **4**: 186. 1900.

F. ampla Greene, *ibid.*

F. speciosa Dougl. var. *stenosepala* Rydb. in Bull. Torr. Bot. Club **31**: 632. 1905.

F. speciosa Dougl. var. *angustifolia* Rydb. *ibid.*

F. stenosepala Rydb. *ibid.* **33**: 149. 1906; Wooton & Standl. in Contr. U. S. Nat. Herb. **19**: 500. 1915.

F. angustifolia Rydb. in Bull. Torr. Bot. Club **33**: 149. 1906.

Tessaranthium macrophyllum (Greene) Rydb. Fl. Rocky Mts. 666. 1917, and ed. 2, 666. 1922.

T. speciosum (Dougl.) Rydb. *ibid.*

T. scabrum (Jones) Rydb. *ibid.*

T. stenosepalum Rydb. *ibid.*

T. angustifolium Rydb. *ibid.*

Biennials or short-lived perennials from a thickened, somewhat woody tap-root; stem 0.3–2 m. high, erect, unbranched, foliose, terete, glabrous to scabrous; leaves in whorls of 3–4, membranous, entire, strongly parallel-veined, usually somewhat scabrous or puberulent, occasionally glabrous or glabrate; the basal leaves oblong to oblanceolate, spatulate, 25–50 cm. long, 3–9 cm. broad, gradually narrowed into an obscure, winged petiole; the cauline leaves sessile, linear to oblong-lanceolate, 5–15 cm. long, 1–2.5 cm. broad; inflorescence a terminal, cymose, fasciculate panicle; the pedicels clustered, 1–8 cm. long; the bracts opposite or 3–4-whorled, linear to lanceolate, 2–10 cm. long; calyx-lobes nearly distinct, linear to lanceolate, subulate, 1.5–2.5 cm. long; corolla-lobes deeply cleft, ovate to oblong-ovate, 1.5–2.5 cm. long, 0.5–

0.8 cm. broad, usually somewhat tapered at the apex, white or somewhat greenish, frequently maculate, bearing a pair of fimbriate, oblong foveae upon the ventral surface; fringe of the crown 3–5 mm. long, almost equalling the length of the foveae; capsule 2–2.5 cm. long, 1–1.5 cm. broad, partially enclosed within the persistent perianth, compressed contrary to the valves.

Distribution: from the Black Hills of South Dakota, south to New Mexico, west to California, Oregon, and Washington. A montane species occurring chiefly at altitudes from 5000–9000 feet.

Specimens examined:

South Dakota: Piedmont, 1893, *Pratt* (C); Black Hills National Forest, 15 June 1910, *Murdoch 4098* (F).

Montana: July 1894, *Mrs. Moore* (M); Belt Mountains, 12 July 1860, *Hayden* (M); Henry's Lake and Mt. Chauvet, 29 July 1897, *Rydberg & Bessey 4698* (F); Helena, June 1891, *Kelsey* (F); Helena, July 1892, *Starz* (F); head of Prickly Pear Creek, July 1883, *Scribner 156* (F, G).

Wyoming: Laramie Peak, Albany Co., open foothills, 10 July 1900, *A. Nelson 7516* (M, G); Medicine Bow Mt., Aug. 1856, *H. Engelmann* (M); Mammoth Hot Springs, moist open slopes, 1 July 1899, *Nelson & Nelson 5629* (M, G); Jackson's Hole, 21 Aug. 1894, *A. Nelson 935* (M, G); French Creek, near Laramie, 28 June–1 Aug. 1899, *Pammel 42* (M); head of Powder River and along Big Horn Mountains, Sept. 1859, *Hayden* (M).

Colorado: Estes Park, Larimer Co., 16 June 1916, *E. L. Johnston 770B* (M); rocky banks near Tolland, Gilpin Co., 25 June 1926, *E. J. Palmer 31322* (M); Rollinsville, dry open plains, alt. 8500 ft., 9 July 1913, *Overholts* (M); Tongue Creek, Mesa, Delta Co., alt. 8000–9000 ft., Aug. 1892, *Purpus 304* (M); The Crags, 14 July 1901, *Clements & Clements 192* (M, G); mountains, Larimer Co., 1 July 1896, *Crandall* (M); Camerons Cove, Aug. 1900, *Harper & Harper 4959* (F); mountain-sides near Empire, 3 Aug.–8 Sept. 1892, *Patterson 243* (G, F, M); South Park, June 1873, *Wolf* (F); Keblar Pass, 14 Aug. 1901, *C. F. Baker 947* (M); Bob Creek, W. La Plata Mts., alt. 10,000 ft., 30 June 1898, *Baker, Earle & Tracy 271* (M, F, G); from the head-waters of Clear Creek and the alpine ridge lying east of "Middle Park," 1861, *Parry 310* (M, G); Ute Pass, 30 June 1886, *Trelease* (M);

arid slopes of Douglas Mt., Empire, 12 Aug. 1874, *G. Engelmann* (M); flank of Snowy Range, wet mountain valleys, alt. 9000 ft., 24 July 1872, *Redfield* (M); rocky summits above Idaho, alt. 8000–8500 ft., 31 July 1874, *G. Engelmann* (M); Stove Prairie Hill, 1 July 1896, *Crandall 1490* (F); Pike's Peak, 1890, *Carleton* (C); region of Pike's Peak, alt. 6000–13000 ft., July–Aug. 1912, *Brumbach & Davies 115* (F); near Manitou, alt. 7200 ft., 11 July 1884, *Letterman 309* (M, F); river bottom, Bayfield, 9 Aug. 1917, *Payson & Bethel 1153* (M); Middle Mountains, 1862, *Hall & Harbour 553* (F); Pagosa Springs, 25 July 1899, *C. F. Baker 524* (G); near Pagosa Peak, alt. 10000 ft., Aug. 1899, *C. F. Baker 525* (M); Keblar Pass, alt. 10000 ft., 14 Aug. 1901, *C. F. Baker* (G).

New Mexico: Winsor Creek, in the Pecos River National Forest, alt. 8600 ft., 29 June 1908, *Standley 4034* (F, G); in and around the south end of the Black Range, Kingston, Sierra Co., alt. 6600 ft., 13 July 1904, *Metcalfe 1160* (M, G); vicinity of Las Vegas, San Miguel Co., Aug. 1923, *Anect 134* (M); Hermits Peak, Aug. 1884, *Snow* (M); Sandia Mts., 23 July 1903, *Hedgcock* (M); in forest of Douglas spruce and rock pine, Haynes Canyon, Alamo National Forest, 10 Aug. 1911, *Barlow* (F); in Grant Co., in the vicinity of Silver City, Fort Bayard, Santa Rita, Fierro, and on the GOS Ranch near Hodge's house, 27 Aug.–12 Sept. 1911, *Holzinger* (M); Balsam Park, Sandia Mts., alt. 8200 ft., 4 July 1914, *Ellis 152* (M); in the Mogollon Mts., on or near the west fork of the Gila River, Socorro Co., alt. 7500 ft., 7 Aug. 1903, *Metcalfe 411* (M, G); valley of Santa Fe Creek, June 1847, *Fendler 686* (M).

Idaho: wooded slope, Salmon, Lemhi Co., alt. 5500 ft., 4 July 1920, *Payson & Payson 1893* (M); 4 miles south of Ketchum, 23 July 1895, *Henderson 3558* (M).

Utah: alpine rocky crests, Dyer Mine, Uintah Mts., 5 July 1902, *Goodding 1255* (M, G); in the vicinity of Clayton Peak, Wasatch Mts., alt. 9000 ft., 12–26 Aug. 1903, *Stokes* (M); gravel, Fish Lake, alt. 10000 ft., 2 Aug. 1894, *M. E. Jones 5710* (M); Salt Lake City and vicinity, 7 July 1908, *Clemens* (M, G); American Fork Canyon, alt. 7500 ft., 27 July 1880, *M. E. Jones 1878* (M).

Arizona: Pine, *M. E. Jones* (M); Rincon Mts., 1891, *Neally 81* (M); Willow Spring, July 1874, *Rothrock 251* (M, F); without locality, 1877, *E. Palmer 304* (M); near soldier's camp, Santa Catalina Mts., 13 July 1916, *Harris C. 16296* (M); moist soil, Huachuca Mts., alt. 8000 ft., 8 July 1884, *Pringle* (M, G); in the vicinity of Flagstaff, alt. 7000 ft., 5 July 1898, *MacDougal 236* (M, G); Chiricahua Mts., alt. 8500 ft., 13 Aug. 1907, *Blumer 1619* (M).

Washington: Yakima region, 1882, *T. S. Brandegee 14840* (M).

Oregon: moist borders of pine woods, Bates Lumber Co., near Austin, E. Grant Co., 5 June 1925, *Henderson 5324* (M, G); Steins Mts., opposite Devine Ranch, along streams, alt. 1890 m., 7 July 1896, *Leiberg 2426* (M, G).

California: Faith Valley, Alpine Co., alt. 8000 ft., Aug. 1892, *Hansen 595* (M); south fork of San Joaquin River, alt., 9000 ft., July 1900, *Hall & Chandler 716* (M); near Yosemite, Sierra Nevada, 1875, *Muir 5024* (M); about Summit Lake, near the summit of Mt. Sanhedrin, 15 July 1902, *A. A. Heller 5883* (M, G); without locality, 186–, *Bolander 6361* (G).

2. **F. caroliniensis** Walt. Fl. Carol. 87. 1788; Torr. Fl. N. & M. US. 187. 1824; Torr. Fl. N. Y. **2**: 109. 1843; Gray, Man. Bot., ed. 7, 659. 1908. Pl. 14, fig. 6.

Swertia difformis L. Sp. Pl. ed. 1, **1**: 226. 1753, and ed. 2, **1**: 328. 1762.

Frasera Walteri Michx. Fl. Bor.-Am. **1**: 97. 1803; Barton, Veg. Mat. Med. U. S. **2**: 103. 1818; Ell. Sketch Bot. S. Car. & Ga. 205. 1824; Darby, Bot. S. States, 437. 1855.

F. officinalis Barton, Fl. Virg. 49. 1812.

Swertia Frasera Sm. in Rees, Cycl. **34**: 1819.

Frasera verticillata Raf. Med. Fl. **1**: 196. 1828.

"*Frasera carolinensis* Walt." acc. to Hook. Fl. Bor.-Am. **2**: 66. 1840; Chapman, Fl. S. U. S. ed. 2, 357. 1889; Small, Fl. S. E. U. S. 931. 1903, and ed. 2, 931. 1913; Britt. & Brown, Ill. Fl. **3**: 15. 1913.

Sweertia carolinensis O. Ktze. Rev. Gen. **2**: 430. 1891.

Perennials from a much-thickened, somewhat woody tap-root; stem 1–1.5 m. high, erect, unbranched, foliose, terete, glabrous; leaves in whorls of 3–5 (usually 4), membranous, entire, penni-

nerved, glabrous; the basal leaves obovate to oblanceolate, 20–35 cm. long, 4–8 cm. broad, gradually narrowing into an obscure petiole; the cauline leaves sessile, oblong-lanceolate, 5–20 cm. long, 1–5 cm. broad; inflorescence a terminal, compound, open paniculate cyme; the peduncles clustered, 4–12 cm. long; the foliaceous bracts opposite or 3–4-whorled, lanceolate, 2–10 cm. long; calyx-lobes nearly distinct, lanceolate, mucronate, somewhat subulate, 20 mm. long, 2 mm. broad; the corolla-tube shallow, lacking a conspicuous crown; the lobes deeply cleft, ovate, 10–20 mm. long, 4 mm. broad, tapered at the apex, light greenish-yellow, marked with small brown-purple dots, bearing on the ventral surface a single, circular, fimbriate fovea; capsule 2 cm. long, 1 cm. broad, flattened parallel to the valves, partially enclosed within the persistent perianth; seeds dark brown, oblong, 0.9–1 cm. long, 0.4–0.5 cm. broad, pitted, conspicuously winged.

Distribution: from the Carolinas north to Michigan and west to Missouri. A species usually occurring in rich soil of open woodlands.

Specimens examined:

North Carolina: mountains of North Carolina, 1878 (F).

Georgia: Estatoah Falls on Mud Creek, Rabun Co., alt. 3000 ft., 12 Aug. 1893, *Small* (M, F).

Alabama: Lookout Mt., Collinsville, De Kalb Co., 29 June 1897, *Eggert* (M).

Mississippi: Agric. College, Oktibbeha Co., 10 May 1892, *Tracy 1348* (M).

Michigan: dry open woods, Kalamazoo Co., 27 July 1874, *Tuthill 9* (F); roadsides, Jackson Co., 22 June 1897, *Camp & Camp* (M, F); Jackson Co., 11 June 1897, *Camp & Camp* (M).

Indiana: Hanover, May 1882, *Young* (M).

Kentucky: margins of woods, along small streams, near Dawson Springs, Caldwell Co., 29 May 1920, *E. J. Palmer 17689* (M); rocky fields, roadsides, Bowling Green, 1 June 1893, *Price* (M).

Tennessee: open woods, Lookout Mt., near Chattanooga, 17 May 1911, *Churchill 659* (M); wooded slope, Lookout Mt., near Chattanooga, 20 May 1911, *Churchill* (M).

Illinois: Carbondale, 1871, *French* (M); rocky hills, Belknap, Pulaski Co., 13 May 1919, *E. J. Palmer 15132* (M); open woods about Belleville, May 1846, *Hilgard* (M); open woods east of Belleville, June 1834, *G. Engelmann 441* (M); Carbondale, 31 May 1885, *Wislizenus 343* (M).

Missouri: Big River, near Irondale, 24 May 1924, *Drushel* (M); Iron Mountain Lake, Iron Co., 28 May 1921, *Drushel* (M); rocky hills near Big River, St. Francois Co., 3 July 1892, *Eggert* (M); woods near Mine La Motte, Madison Co., 23 June 1898, *Eggert* (M); Bonne Terre, 31 Aug. 1891, *Eggert* (M); dry prairies, near Woodlawn, Jefferson Co., 16 May 1898, *Eggert* (M); De Soto, Jefferson Co., 25 May 1896, *Eggert* (M); rocky hillsides, Jefferson Co., 25 May 1896, *Eggert* (M); rocky hills, near Big River, St. Francois Co., 31 Aug. 1891, *Eggert* (M); "Stony hills," St. Francois Co., 31 Aug. 1891, *Eggert* (M); sandy ground, Scott Co., 20 May 1894, *Eggert* (M); rocky hillsides, near Big River, 31 Aug. 1891, *Eggert* (M); Mine La Motte, Madison Co., 19 May 1927, *Greenman, Larsen & Beardsley* (M); Iron Mountain Lake, 31 May 1925, *Kellogg 1931* (M); open woods along small streams, near Bismarck, St. Francois Co., 25 June 1920, *E. J. Palmer 18075* (M); 10 July 1887, *Hasse* (F); roadside, Des Arc, Iron Co., 6 May 1908, *H. H. Smith 405* (F); rocky, wooded hillsides near Shirley, Washington Co., 29 May 1924, *E. J. Palmer 25210* (M); Big River, Desloge and Bonne Terre, 28 Aug. 1898, *Trelease 1130* (M).

3. **F. fastigiata** (Pursh) Heller in Bull. Torr. Bot. Club **24**: 312. 1897; Piper in Contr. U. S. Nat. Herb. **11**: 451. 1906; Piper & Beattie, Fl. S. E. Wash. 193. 1914. Pl. 14, fig. 11.

Swertia fastigiata Pursh, Fl. Am. Sept. 101. 1814.

Frasera thyrsiflora Hook. Lond. Jour. Bot. **3**: 288. 1851; Gray, Syn. Fl. N. Am. **2**[1]: 125. 1878; Howell, Fl. N. W. Am. 448. 1897.

"*Sweertia fastigiata* Pursch" acc. to O. Ktze. Rev. Gen. **2**: 430. 1891.

Biennial or short-lived perennial from a thickened tap-root; stem 6–10 dm. high, erect, unbranched, foliose, terete, glabrous; leaves usually in whorls of 3, entire, membranous, penninerved,

glabrous; the basal leaves broadly obovate to oblanceolate, 15–30 cm. long, 5–10 cm. broad, narrowing into an obscure petiole; the cauline leaves subsessile, obovate, 4–12 cm. long, 1.5–6 cm. broad; inflorescence a terminal, interrupted, fasciculate, cymose panicle; the peduncles clustered, 2–6 cm. long; the bracts opposite, or 3–4-whorled, lanceolate, 2–10 cm. long; calyx-lobes almost distinct, somewhat subulate, 2 cm. long, 0.2 cm. broad; corolla-tube shallow, lacking a conspicuous crown; the lobes deeply cleft, oblong-lanceolate, 0.8–1. cm. long, 0.3 cm. broad, acute, pale blue, bearing on their ventral surfaces single, circular, fimbriate foveae; capsule 1.5 cm. long, 0.5 cm. broad, flattened parallel to the valves, partially enclosed within the persistent perianth; seeds oblong to oval or roughly triangular, 0.5–0.6 cm. long, 0.3 cm. broad, pitted or rugose, usually winged.

Distribution: northern Idaho and adjacent Washington.

Specimens examined:

IDAHO: on gravelly open hillsides, Moscow Hills, Latah Co., 25 June 1896, *Elmer 340* (M); Cedar Mts., Latah Co., June 1899, *Elmer 1688* (M); pine groves of foothills, Kamiac Buttes, June 1897, *Elmer 802* (M); Thatuna Hills, 5 July 1926, *Epling & Houck 9147* (M); about Lake Waha, Nez Perces Co., alt. 2000–3500 ft., 24 June 1896, *Heller & Heller 3285* (M); near Moscow and St. Maries R., 26 May–8 Aug. 1894, *Henderson 2271* (G); in low, rich woods, Kootenai Co., June 1891, *Leiberg 213* (M); Santianne Creek bottom, alt. 980 m., 25 June 1895, *Leiberg 1064* (M, G); Cedar Mts., Latah Co., 16 July–7 Aug. 1893, *Piper 1618* (M, F, G); meadows, Kootenai Co., June 1892, *Sandberg* (M); rich moist woods, Kootenai Co., June 1880, *Sandberg* (M, F); vicinity of Lake Waha, Nez Perces Co., 23 May 1892, *Sandberg, MacDougal & Heller 239* (F, G); base of mountains, near the Clearwater, 26 Aug. 1880, *Watson 270* (G).

WASHINGTON: Spokane Co., 1892, *Henderson 2271* (G); Clearwater, *Spalding* (G); damp grounds in open woods, Spokane Co., 5 June 1889, *Suksdorf 938* (F, M); damp grounds in open woods, Spokane Co., 5 June 1889, *Suksdorf 939* (G).

4. **F. neglecta** Hall in Bot. Gaz. **31**: 388. 1901. Pl. 14, figs. 8, 12.
Swertia neglecta (Hall) Jepson, Man. Fl. Pl. Calif. 766. 1925.

Perennial from a rhizome; stem 3.0–4.0 dm. high, erect, unbranched, subscapose, terete, glabrous; leaves opposite, subcoriaceous, glabrous; the basal leaves almost sessile, linear, 5–18 cm. long, 0.4–0.8 cm. broad, with white, somewhat serrate, crisped margins, becoming entire towards the apex; the cauline leaves sessile, linear, 3–8 cm. long, 0.4–0.6 cm. broad; inflorescence an elongated, interrupted, fasciculate cyme; the peduncles clustered, 1–12 cm. long; the bracts foliaceous, somewhat scarious, sessile, linear, 2–10 cm. long, distinct or united at the base; calyx-lobes nearly distinct, conspicuously subulate, 0.5 cm. long, 0.1 cm. broad, scarious-margined; the corolla-tube shallow, lacking a conspicuous crown; corolla-lobes deeply cleft, oblong, acuminate, 0.8–1 cm. long, 0.4 cm. broad, greenish-white, purple-veined, bearing on the ventral surface an oblong fovea, the lower part of the fovea often continuous with the tissue of the petal, sometimes 2-toothed or 2-lobed, the upper part saccate with the marginally fimbriate, circular orifice somewhat raised above the petal-surface; capsule flattened parallel to the valves, partially enclosed within the persistent perianth.

Distribution: California, chiefly along the northern slopes of the San Bernardino Mountains.

Specimens examined:

California: Swartout Canyon, desert slopes of the San Gabriel Mountains, alt. 6500 ft., 5 July 1908, *Abrams & McGregor 628* (G); Acton, Mt. Gleason, Los Angeles Co., June 1902, *Elmer 3609* (G); north fork, Mt. Pinos, Ventura Co., alt. 1750 m., 28 June 1905, *H. M. Hall 6462* (C, F); Swartout Canyon, alt. 6860 ft., 3–6 June 1900, *H. M. Hall 1495* (M, F, G, C type); Holcomb Valley, San Bernardino Mts., alt. 8000 ft., June 1886, *Parish & Parish* (C); dry ridges, Holcomb Valley, San Bernardino Mts., Aug. 1882, *Parish & Parish 1474* (G); Holcomb Valley, San Bernardino Mts., alt. 7300 ft., 16 June 1916, *S. B. Parish 10921* (C).

5. F. montana Mulford in Bot. Gaz. **19:** 119. 1894.

Pl. 14, fig. 15.

Leucocraspedum montanum (Mulford) Rydb. Fl. Rocky Mts. 665. 1917, and ed. 2, 665. 1922.

Perennial from rhizomes; stem 3.0–4.5 dm. high, 0.3–1 cm. thick at the base, erect, unbranched, subscapose, terete, glabrous; leaves opposite, entire, membranous, parallel-veined, glabrous; basal leaves narrowly oblanceolate, 3–12 cm. long, 0.3–0.5 cm. broad; cauline leaves linear, 3–12 cm. long, 0.2–0.3 cm. broad; inflorescence a terminal fasciculate cyme, about 3 cm. broad; peduncles clustered, 1–3 cm. long; bracts opposite, foliaceous, 2–4 cm. long; calyx-lobes almost distinct, narrowly subulate, 0.5 cm. long, 0.1 cm. broad; corolla-tube shallow, corona small, deeply cut into two or more setae; the lobes deeply cleft, oblong, somewhat acute, 0.8 cm. long, 0.2–0.3 cm. broad, creamy white, bearing on the ventral surface a single obovate, fimbriate, basally saccate fovea; capsule flattened contrary to the valves, partially enclosed within the persistent perianth.

Distribution: known only from "mountain beyond Pioneer," Idaho.

Specimens examined:

IDAHO; Pioneer, alt. 5000 ft., 26 July 1892, *Mulford* (F TYPE); mountain beyond Pioneer, 23 July 1892, *Mulford* (M, G).

6. **F. nitida** Benth. Pl. Hartw. 322. 1839; Brew. & Wats. Bot. Calif. 484. 1876; Gray, Syn. Fl. N. Am. 2[1]: 126. 1878; Howell, Fl. N. W. Am. 448. 1897; Piper in Contr. U. S. Nat. Herb. **11**: 452. 1906. Pl. 14, figs. 13, 14.

Swertia nitida (Benth.) Jepson, Man. Fl. Pl. Calif. 766. 1925.

Frasera nitida Benth. var. *albida* Suksdorf, Werdenda **1**: 30. 1927.

Perennial from a branching somewhat woody rhizome; stems 25–50 cm. high, 0.2–0.3 cm. in diameter at the base, erect, unbranched, subscapose, terete, glabrous; leaves opposite, entire, often conspicuously white-margined, parallel-veined, glabrous; the basal leaves spatulate to sublinear, 5–25 cm. long, 0.5–1 cm. broad; cauline leaves sessile, narrowly oblanceolate to sublinear, 5–10 cm. long, 0.3–0.5 cm. broad; inflorescence a terminal, interrupted, racemose cyme; peduncles clustered, 0.5–4 cm. long; bracts opposite, foliaceous, sublinear, 4–12 cm. long; calyx-lobes nearly distinct, somewhat subulate, tapering to a sharp point, 0.6–0.7 cm. long; corolla-tube shallow with a conspicuous peta-

loid corona; the lobes ovate to oblong, acute, 0.7–0.8 cm. long, 0.3 cm. broad, greenish, bearing on their ventral surfaces single, oblong, deeply fringed, saccate foveae; capsule 1.5 cm. long, 0.5 cm. broad, flattened parallel to the valves, partially enclosed within the persistent perianth; seeds few, often only four, oblong, 0.7 cm. long, 0.3 cm. broad, closely appressed, brown, thick-margined, wingless, pitted.

Distribution: western Idaho, west to southern Washington, south to southern California.

Specimens examined:

Idaho: dry stony hills near Cuprum, 10 July 1899, *Cusick 2226* (C, F, G).

Washington: Klickitat, June 1879, *Howell* (M); Klickitat Co., 27 May–Aug. 1881, *Suksdorf 40* (G); hillsides, W. Klickitat Co., 27 May, *Suksdorf 161* (F); hillsides, W. Klickitat Co., 27 May 1881, *Suksdorf* (C).

Oregon: dry prairies, eastern Oregon, July 1880, *Howell* (F); open grassy hillsides, 13 May 1924, *Henderson 467* (M); Dalles, Wasco Co., 23 May 1910, *A. A. Heller 10087* (G); Siskiyou Mts. 19 Aug. 1880, *G. Engelmann* (M); Woodville, Jackson Co., 5 July 1893, *Hammond 277a* (M); near camp by Grizzly Butte, Crook Co., alt. 840 m., 14 June 1891, *Leiberg 227* (G, C); Oregon Boundary Commission, Columbia River, lat. 46–49° N., *Lyall 1860* (G); dry ground along Silvies River at mouth of Emigrant Creek, Harney Co., 25 June 1912, *Peck 4501* (F); Odessa, Short Creek Hill, Klamath Co., alt. 4200 ft., 30 June 1910, *Rose 1624* (M).

California: Plumas Co., *Mrs. R. M. Austin* (F); gravelly red soil, alt. 4500 ft., 20 July 1893, *M. S. Baker* (C); Morley's Station, Shasta Co., 22 May 1894, *M. S. Baker & Nutting* (C); Cherokee, Butte Co., May 1879, *Bidwell* (G); Battle Rock Mt., Lake Co., 1 July, *K. Brandegee* (C); Prattsville, Plumas Co., 9 July 1892, *T. S. Brandegee* (C); south side of Mt. Shasta, Siskiyou Co., alt. 5000–10000 ft., 15–31 July 1897, *H. E. Brown 545* (F); dry land near Yreka, Siskiyou Co., 2 June 1910, *Butler* (C, M); Klamath River, Humboldt Co., alt. 1400 ft., June 1901, *Chandler 1486* (C, M); Hupa Indian Reservation, alt. 500 ft., June 1901, *Chandler 1383* (C); Castle Lake Trail, Shasta Region, Aug. 1910, *Congdon*

(C); lower slopes of Hoopa Mt., Humboldt Co., on the borders of Supply Creek, 21 June 1899, *Davy 5737* (C); Cantara, Siskiyou Co., 28 Aug. 1912, *Eastwood 1945* (G); Nevada City, Nevada Co., 20–22 June, 1912, *Eastwood 582* (C); Goose Valley, Shasta Co., 29 June–11 July 1912, *Eastwood 950* (G); Scotts Mt., alt. 5000–7000 ft., 30 Aug. 1880, *G. Engelmann* (M); near Yreka, Siskiyou Co., 14 June 1876, *Greene 856* (M); lava beds of northeastern Shasta Co., alt. 4000 ft. alt., June 1903, *Hall & Babcock 4241* (C); Cobb Mt., 500 ft. below summit, 28 July 1913, *Hall 9594* (M, G, F, C); Bear River, Nevada County, alt. 1400 ft., 5 June 1916, *Hall 10157* (C); Coffee Creek Canyon, Salmon Mts., Trinity Co., alt. 1260 m., 16 July 1909, *Hall 8546* (G, M, F); Pitt River Canyon, alt. 1000 ft., June 1903, *Hall & Babcock 4006* (C); near Nash Mine, alt. 4100 ft., 16 July 1909, *Hall 8546* (C); near Redding, Shasta Co., 27 May 1905, *A. A. Heller* (C); grade between Greenville and Prattsville, Plumas Co., 12 July 1907, *Heller & Kennedy 8820* (G); near Redding, Shasta Co., 27 May 1905, *A. A. Heller 7879* (G); dry gravelly slope, north side of Mt. Eddy, Siskiyou Co., alt. 4500 ft., 16 July 1915, *A. A. Heller 12103* (F, M); Mt. Hanna, Lake Co., 15 July 1897, *Jepson* (G); near Prattsville, at Mt. Meadow, alt. 5500 ft., 2 July 1897, *M. E. Jones* (M); Redding, 16 May 1910, *W. W. Jones 222* (G); Sierra Co., 1874, *J. G. Lemmon* (C 174108); Holcomb Valley, San Bernardino Mts., alt. 8000 ft., Aug. 1882, *Parish & Parish 1474* (F); Redding, Shasta Co., 24 May 1913, *L. E. Smith 235* (G); Cobb Mt. on south side, alt. 2000 ft., 12 July 1905, *J. P. Tracy 2244* (C); Trinity Co., June 14, *Yates 19385* (C).

6a. Var. **albicaulis** (Dougl.) Card, n. comb. Plate 14, fig. 9.

Frasera albicaulis Dougl. ex. Griseb. in Hook. Fl. Bor.-Am. **2**: 67. 1840; Gray in Syn. Fl. N. Am. **2**^{1}: 126. 1878; Howell, Fl. N. W. Am. **1**: 449. 1897; Piper & Beattie, Fl. S. E. Wash. 193. 1914.

"*Frasera albicaulis* Griseb." Gen. et Sp. Gent. 330. 1839; in DC. Prodr. **9**: 131. 1845.

Sweertia albicaulis Dougl. ex O. Ktze. Rev. Gen. **2**: 430. 1891.

Leucocraspedum albicaule Dougl. acc. to Jepson, Man. Fl. Pl. Calif. 766. 1925.

Frasera albicaulis Dougl. f. *alba* St. John in Proc. Biol. Soc. Wash. **41**: 196. 1928.

Plant more or less puberulent; corolla with a more linear fovea.

Distribution: northwestern Idaho, eastern Washington, and northern Oregon.

Specimens examined:

Idaho: Palouse Country and about Lake Coeur d'Alene, June, July 1892, *Aiton* (M); in the vicinity of Moscow, Latah Co., 16–20 June 1892, *A. A. Heller* (F); Upper Ferry, Nez Perces Co., May 1896, *Heller & Heller* (F); about Lewiston, Nez Perces Co., alt. 900 ft., 20 May 1896, *Heller & Heller* (M); open hillsides, Salmon, Lemhi Co., alt. 5000 ft., 27 June 1920, *Payson & Payson 1796* (M); meadows, valley of Clearwater River, Nez Perces Co., 3 May 1892, *Sandberg, MacDougal & Heller 101* (M, F); moist places, Kootenai Co., June 1887, *Sandberg* (F).

Washington: on dry hillsides, Pullman, Whitman Co., May 1897, *Elmer 823* (M); grassy hillsides, head of Hotwai Creek, Whitman Co., 27 May 1928, *English 994* (M); Pullman, 20 June 1893, *Piper 1619* (M); Spokane Co., June 1884, *Suksdorf* (F); prairies, Spokane Co., June 1884, *Suksdorf* (F).

Oregon: slightly moist ground, 10 miles north of Bonanza, Klamath Co., 24 June 1927, *Peck 15174* (M); cattle camp at head of Horse Creek, Wallowa Co., alt. 5400 ft., 24 June 1897, *Sheldon 8344* (M); dry ground near the Dalles, 2 July 1927, *Thompson 2851* (M).

6b. Var. **Cusickii** (Gray) Card, n. comb.

Plate 14, fig. 10; pl. 15, fig. 1.

Frasera Cusickii Gray in Proc. Am. Acad. **22:** 310. 1887; Howell, Fl. N. W. Am. 448. 1897.

Stems generally shorter than in the species, 15–20 cm. high; flowers larger, corolla-lobes 0.8–1 cm. long, 0.4 cm. broad.

Distribution: Idaho and Oregon.

Specimens examined:

Idaho: open hillsides, Salmon, Lemhi County, alt. 5000 ft., 27 June 1920, *Payson & Payson 1796* (M).

Oregon: hillsides of Grande Ronde Valley, 1886, *Cusick 1427* (G type); stony hillsides near Union, May 1886, *Cusick 1427* (C); sterile, stony ridges, southern Blue Mts., alt. 4000–5000 ft., June 1897, *Cusick 1635* (C, F, M); mountain sides of Grande Ronde Valley, near Union, 6 June 1898, *Cusick 1920* (F, G, M, C).

7. **F. coerulea** Mulford in Bot. Gaz. **19**: 118. 1894.

Leucocraspedum coeruleum (Mulford) Rydb. Fl. Rocky Mts. 666. 1917, and ed. 2, 666. 1922.

Perennial from a branching rhizome; stem 1.5–2.5 dm. tall, erect, unbranched, foliose, terete, glabrous; leaves opposite, entire, membranous, white-margined, parallel-veined, glabrous; basal leaves narrowly oblanceolate, 5–20 cm. long, 0.5–1 cm. broad, petiole inconspicuous; cauline leaves sessile, linear, 4–8 cm. long, 5–6 cm. broad; inflorescence closely paniculate; pedicels 0.5–3 cm. long, 2–4 in the axils; calyx-lobes nearly distinct, slightly subulate, 0.5–0.7 cm. long, 1 mm. broad, scarious-margined; corolla-tube deeply cleft, corona conspicuous, petaloid, nearly as long as the fovea; corolla-lobes ovate, acute, 6–8 mm. long, bearing upon the ventral surface a fimbriate, linear fovea; capsule and seed not seen.

Distribution: Owyhee Mts., in southeastern Idaho, and Oregon.

Specimens examined:

IDAHO: Owyhee Mts., near Wagonville, alt. 7000 ft., 8 July 1892, *Mulford* (M, G, COTYPES); dry open slopes, De Lamar, Owyhee Co., alt. 7000 ft., 22 June 1911, *Macbride 961* (M, G, F).

OREGON: near camp by Grizzly Butte, Crook Co., alt. 840 m., 14 June 1894, *Leiberg 227* (M): head of Otis Creek, Blue Mts., 11 June 1897, *Cusick 1635* (G).

8. **F. tubulosa** Coville in Proc. Biol. Soc. Wash. **7**: 71. 1891. Pl. 14, fig. 5.

Swertia tubulosa (Coville) Jepson, Man. Fl. Pl. Calif. 767. 1925.

Biennial or short-lived perennial from a tap-root; stem about 6 dm. high, .6–1.0 cm. thick at the base, erect, unbranched, subscapose, terete, glabrous, glaucous; leaves in whorls of 5 or 6, entire, membranous, narrowly white-margined; basal leaves spatulate to oblanceolate, 4–9 cm. long, 1 cm. broad, obtuse, mucronate; inflorescence a terminal, narrow, spicate panicle 2–5 dm. long, interrupted below; the pedicels erect, 1–5 cm. long; bracts opposite, linear, 7–10 cm. long; calyx-lobes nearly distinct, linear, subulate, 0.6–0.8 cm. long; corolla-tube shallow; the lobes oblong-obovate, 0.8–1 cm. long, 0.2 cm. broad, acuminate, white,

bearing tubular foveae half as long as the corolla and saccate at the base, longitudinally 2-cleft at the apex; capsule oblong-lanceolate, 1 cm. long, .5 cm. broad, compressed parallel to the valves; seeds 6–10, oblong, flat and thin.

Distribution: Tulare and Inyo Counties, California.

Specimens examined:

California: summit, west Olancha, Inyo Co., 21 June 1899, *S. W. Austin 117* (C); Kern River, Tulare Co., 3 Aug. 1904, *Culbertson 4329* (M, F, G); Kern River, Tulare Co., 3 Aug. 1904, *Eastwood 4329* (C); near Lion Meadow, basin of upper Kern River, Tulare Co., July 1904, *Hall & Babcock 5401* (C); Soda Springs, basin of upper Kern River, alt. 6300 ft., Tulare Co., July 1904, *Hall & Babcock 5412* (C); southwest side of Olancha Mountain, alt. 8500 ft., Tulare Co., 25–30 June 1904, *Hall & Babcock 5271* (C); plains along the Kern River, alt. 6000–7000 ft., Aug. 1895, *Purpus 1407* (C).

9. F. puberulenta Davidson in Bull. So. Calif. Acad. Sci. 11: 77. 1912. Pl. 14, fig. 7; pl. 15, fig. 2.

Perennial from a somewhat thickened tap-root; stem about 2.5 dm. high, erect, unbranched, foliose, closely puberulent throughout; leaves opposite, entire, white-margined, coriaceous, parallel-veined, puberulent; the basal leaves obovate, 5–10 cm. long, 1–5 cm. broad, gradually narrowing into a relatively long winged petiole; cauline leaves narrowly elliptical, 3–5 cm. long, 1.5 cm. broad; inflorescence a terminal somewhat open thyrsiform cyme; the peduncles clustered, 3–5 cm. long; the bracts opposite, foliaceous, 1–5 cm. long; calyx-lobes nearly distinct, narrowly lanceolate, slightly subulate, 1–1.5 cm. long, 2 mm. broad; corolla-tube shallow, crown lacking; the lobes oblong, 7 mm. long, 3 mm. broad, mucronate-setose, greenish white, conspicuously purple-dotted, bearing on the ventral surface a single oblong fimbriate fovea, saccate-sagittate at the base; capsules not seen.

Distribution: Inyo County, California.

Specimens examined:

California: South Lake, Bishop Creek, Inyo Co., July 1911, *Davidson 2705* (C, LA type).

10. F. Parryi Torr. Bot. Mex. Bound. Surv. 156. 1859; Gray, Syn. Fl. N. Am. **2**[1]: 126. 1878. Pl. 14, fig. 1.

Sweertia Parryi (Torr.) O. Ktze. Rev. Gen. **2**: 430. 1891.

"*Swertia Parryi* (Torr.) Ktze," acc. to Jepson, Man. Fl. Pl. Calif. 767. 1925.

Perennial from a somewhat branched rhizome; stem 7–9 dm. high, erect, unbranched, scapose, terete, glabrous; leaves opposite, entire, more or less conspicuously white-margined, coriaceous, parallel-veined, glabrous; basal leaves subsessile, lanceolate, 10–15 cm. long, 1–2 cm. broad; cauline leaves sessile, lanceolate, 4–8 cm. long, 1–1.5 cm. broad; inflorescence a terminal, open, paniculate cyme; peduncles single in the axils, 4–6 cm. long; bracts opposite, foliaceous, broadly lanceolate, acute, 1–5 cm. long; calyx-lobes nearly distinct, broadly lanceolate, subulate, acute, 1–1.8 cm. long, 0.3–0.6 cm. broad; corolla-tube shallow, the corona reduced to cilia; the lobes ovate, narrowed at the base, 1.5 cm. long, 4–8 mm. broad, greenish-white, purple-dotted, bearing on the ventral surface near the base a single acute, lunate fovea; capsule 1.5–2 cm. long, 5–8 mm. broad, flattened contrary to the valves, partially enclosed within the persistent perianth; seeds oblong, 0.4 cm. long, 0.2 cm. broad, slightly thickened, rugose.

Distribution: southern California.

Specimens examined:

California: between Walker's Ranch and the Jacumba, 1 June 1903, *Abrams 3701* (M, F); Witch Creek, San Diego Co., May 1894, *Alderson* (C); San Pedro Martin, 28 May 1893, *T. S. Brandegee* (C); Laguna Mts., San Diego Co., 20 June 1904, *T. S. Brandegee* (C); Ramona, Oct. 1903, *K. Brandegee* (C); east side of Palomar Mt., alt. 3500 ft., 11 July 1904, *Chandler 5468* (C); Badena, 15 Aug. 1884, *Coulter* (F); in the southeastern part of the Colorado Desert, San Diego Co., July 1890, *Gray* (M); San Diego, 1891, *Gregory* (C); in open pine forests in the vicinity of Strawberry Valley, alt. 5200 ft., July 1901, *Hall 2518* (C, M); Rincon Grade, 29 May 1926, *M. E. Jones* (C); summit of mountain near Crafton, San Bernardino Co., April 1876, *J. G. Lemmon* (F, C); San Bernardino, *J. G. Lemmon* (C); Jacumba Hot Springs, near Monument, 20 May 1894, *Mearns 3242* (M); Cuiamaca

Mts., July 1875, *E. Palmer 229* (M); *Parry & Lemmon 232* (M, F); San Bernardino Co., June 1876, *Parry & Lemmon* (M); foothills, June 1887, *S. B. Parish* (F); dry mesas, alt. 350 m., San Bernardino Valley, 24 May 1909, *S. B. Parish 7084* (C); lower foothills, 29 June 1888, *S. B. Parish* (C); lower hills, alt. 360–400 m., San Bernardino Valley, 24 May 1909, *S. B. Parish 7084* (C); foothills, San Bernardino Mts., 7 June 1892, *S. B. Parish 2415* (F); foothills, San Bernardino Mts., 25 April 1885, *S. B. Parish 312* (C); vicinity of San Bernardino, alt. 100–2500 ft., 12 May 1897, *S. B. Parish* (M); foothills, 15 June 1888, *S. B. Parish* (M); San Jacinto Mt., July 1880, *Parish & Parish 312* (F); open ground, Seven Oaks, San Bernardino Mts., June 1902, *White 2* (C).

11. F. albomarginata Wats. Bot. King Exp. 280. 1871; Gray, Syn. Fl. N. Am. **2**[1]: 126. 1878; Tidestrom in Contr. U. S. Nat. Herb. **25**: 417. 1925. Pl. 14, fig. 3.

Sweertia albomarginata (Wats.) O. Ktze. Rev. Gen. **2**: 431. 1891.

Leucocraspedum albomarginatum (Wats.) Rydb. Fl. Rocky Mts. 665. 1917, and ed. 2, 665. 1922.

"*Swertia albomarginata* (Wats.) Ktze." acc. to Jepson, Man. Fl. Pl. Calif. 766. 1925.

Biennials or short-lived perennials from a thickened, somewhat woody tap-root; stem 2–6 dm. high, erect, unbranched, scapose, terete, glabrous; leaves 3–4-whorled, coriaceous, generally undulate, conspicuously white-margined, parallel-veined, glabrous; basal leaves sessile, oblanceolate, 5–10 cm. long, 0.8–1 cm. broad; cauline leaves sessile, linear, 2–8 cm. long, 0.4–0.8 cm. broad; inflorescence a terminal, corymbose cyme; the peduncles 0.5–10 cm. long, mostly solitary; bracts 1–6 cm. long, usually opposite, sometimes whorled, much-reduced in upper part of inflorescence; calyx-lobes nearly distinct, acute, somewhat subulate, 0.3–0.4 cm. long, 0.2 cm. broad; corolla-tube shallow, crown lacking; the lobes ovate-acuminate, 0.8–1 cm. long, 0.4–0.5 cm. broad, greenish-yellow, bearing on the ventral surface a linear, sparsely fringed obcordate fovea; capsule flattened contrary to the valves, partly enclosed within the persistent perianth; seeds oblong, 0.3–0.4 cm. long, wingless, rugose.

Distribution: southern Colorado to southern California.

Specimens examined:

COLORADO: Mesa Verde, July 1875, *T. S. Brandegee 1249* (C); southwest Colorado, *T. S. Brandegee 1215, 1249* (M); Mesa Verde, July 1889, *Eastwood* (C); rocky cedar barrens at summit of Soda Canyon, Tip-off Trail, Southern Ute Reservation, Montezuma Co., 27 June 1929, *Woodson & Anderson 29006* (M).

UTAH: without locality, 1874, *Parry 203* (G).

NEVADA: Pioche, 31 Aug. 1912, *M. E. Jones* (C); vicinity of Pioche, Lincoln Co., 28 June 1909, *Minthorn* (C).

ARIZONA: Oak Creek, 22 June 1883, *Rusby* (F).

CALIFORNIA: Providence Mts., San Bernardino Co., 6 June 1902, *T. S. Brandegee* (C); without locality, 1887, *E. Palmer 305* (M).

11a. Var. **induta** (Tidestrom) Card, n. comb.

Frasera induta Tidestrom in Contr. U. S. Nat. Herb. **25**: 417. 1925.

Finely glandular-puberulent throughout, in all other essential characters similar to the species.

Distribution: southern Nevada.

Specimens examined:

NEVADA: gravelly slopes, Cottonwood Creek Canyon, alt. 5000–6000 ft., Aug. 1896, *Purpus 3065* (C); Charleston Mts., alt. 5000–6000 ft., May–Oct. 1898, *Purpus 6083* (C); between Owens and Lee Canyon, alt. 7000 ft., 24 July 1913, *A. A. Heller 10981* (M, C, G, F).

12. F. paniculata Torr. in Pacif. R. R. Rept. **4**: 126. 1856; Gray, Syn. Fl. N. Am. ed. 2, **2**[1]: 126. 1886; Wooton & Standl. in Contr. U. S. Nat. Herb. **19**: 500. 1915. Pl. 14, fig. 2.

Sweertia Bigelowii O. Ktze. Rev. Gen. **2**: 431. 1891.

Frasera utahensis Jones, Zoe **2**: 19. 1891; Tidestrom in Contr. U. S. Nat. Herb. **25**: 417. 1925.

Herbaceous, caulescent biennial or short-lived perennial, from a thickened somewhat woody tap-root; stem 7–10 dm. high, erect, unbranched, scapose, terete, glabrous; leaves opposite, entire, coriaceous, parallel-veined, glabrous; basal leaves lanceo-

late-acuminate, 10–20 cm. long, 1.5–4 cm. broad, slightly contracted at the base; the lower cauline leaves opposite, 8–10 cm. long, 1–1.5 cm. broad, clasping at the base; the upper leaves reduced to mere bracts; inflorescence a terminal, open panicle; peduncles usually solitary in the axils; bracts opposite, 2–10 cm. long; calyx-lobes nearly distinct, broadly ovate, 0.4 cm. long, 0.2 cm. broad, either acute or acuminate, whitish-margined; corolla-tube shallow, lacking a conspicuous crown; the lobes oblong-obovate, 1 cm. long, 0.7 cm. broad, tapered at the base, yellowish-green, purple-dotted, bearing on the ventral surface 2 oblong, linear, fimbriate, urn-shaped foveae with a conspicuous apical tooth; capsule 1.5 cm. long, 0.5 cm. broad, flattened contrary to the valves, partially enclosed within the persistent perianth; seeds 10–20, generally oblong, 0.7 cm. long, 0.3 cm. broad, closely appressed, unequally thickened, brown, pitted, rugose or irregularly tuberculate, somewhat winged-margined.

Distribution: New Mexico, Arizona, and adjacent Utah.

Specimens examined:

New Mexico: along road northwest of Lybrook's Trading Post (Haynes), Rio Arriba Co., 4 July 1929, *Mathias 616* (M).

Utah: near Moab, 16 June 1913 (G); Courthouse Wash, *M. E. Jones* (C).

Arizona: sand bluffs, Inscription Rock, Zuni Country, 18 Nov. 1853, *Bigelow* (G type); House Rock, 18 June 1890, *M. E. Jones* (C); in sand on high mesa only, Navajo Reservation, July 1916, *Vorhies 43* (M, C, G); *Voth 80* (F); Pahranagath Mts., 1871, *Searls* (G).

List of Exsiccatae

The distribution numbers are printed in *italics*. The number in parenthesis is the species number used in this revision.

Abrams, L. R. *3701* (10).
Abrams, L. R. & E. A. McGregor, *628* (4).
Aiton, G. B. — (6a).
Alderson, R. D. — (10).
Anect, Bro. *134* (1).
Austin, Mrs. R. M. — (6).
Austin, S. W. *117* (8).
Baker, C. F. *524*, *525*, *947* (1).
Baker, C. F., F. S. Earle & S. M. Tracy *271* (1).
Baker, M. S. — (6).
Baker, M. S. & F. Nutting — (6).
Barlow, B. — (1).
Bidwell, Mrs. J. — (6).
Bigelow, J. M. — (12).
Blumer, J. C. —, *1619* (1).
Bolander, H. N. *6361* (1).

Brandegee, K. — (6); — (10).
Brandegee, T. S. *14840* (1); — (6); — (10); —, *1215*, *1249* (11).
Brown, H. E. *545* (6).
Brumbach, F. M. & C. A. Davies, *115* (1).
Butler, G. B. — (6).
Camp, S. H. & D. R. — (2).
Carleton, M. A. — (1).
Chandler, H. P. *1383*, *1486* (6); *5468* (10).
Churchill, J. R. —, *659* (2).
Clemens, Mrs. J. — (1).
Clements, F. E. & E. S. *192* (1).
Congdon, J. W. — (6).
Coulter, J. M. — (10).
Crandall, C. S. —, *1490* (1).
Culbertson, *4329* (8).
Cusick, W. C. *2226* (6); *1427*, *1920* (6b); *1635* (7).
Davidson, A. *2705* (9).
Davy, J. B. *5737* (6).
Drushel, J. A. — (2).
Eastwood, A. *582*, *950*, *1945* (6); *4329* (8); — (11).
Eggert, H. — (2).
Ellis, C. C. *152* (1).
Elmer, A. D. E. *340*, *802*, *1688* (3); *3609* (4); *823* (6a).
English, C. Jr., *994* (6a).
Engelmann, G. — (1); — (2); — (6).
Engelmann, H. — (1).
Epling, C. C. & M. Houck, *9147* (3).
Fendler, A. *686* (1).
French — (2).
Goodding, L. N. *1255* (1).
Gray, I. J. — (10).
Gregory, Mrs. — (10).
Greene, E. L. *856* (6).
Greenman, J. M., E. Larsen & M. Beardsley — (2).
Hall, E. & J. P. Harbour *553* (1).
Hall, H. M. *1249*, *1495*, *6462*, *6485*, *6534*, *6706* (4); *8546*, *9594*, *10157* (6); *2518* (10).
Hall, H. M. & E. B. Babcock *4006*, *4241* (6).
Hall, H. M. & H. D. Babcock *5271*, *5401*, *5412* (8).
Hall, H. M. & H. P. Chandler *716* (1).
Hammond, E. W. *277A* (6).
Hansen, G. —, *595* (1).
Harper, E. T. & S. A. *4959* (1).
Harris, J. A. *C. 16296* (1).
Hasse, H. E. — (2).
Hayden, F. V. — (1).
Hedgecock, G. G. — (1).
Heller, A. A. *5883* (1); —, *7879*, *10087*, *12103* (6); —, (6a); *10981* (11a).
Heller, A. A. & G. *3285* (3); — (6a).
Heller, A. A. & P. B. Kennedy, *8820* (6).
Henderson, L. F. *3558*, *5324* (1); *2271* (3); *467* (6).
Hilgard, T. — (2).
Holzinger, J. M. — (1).
Howell, T. J. — (6).
Jepson, W. L. — (6).
Johnston, E. L. *770B* (1).
Jones, M. E. —, *5710*, *1878* (1); — (6); — (10); — (11); — (12).
Jones, W. W. — (1); *222* (6).
Kellogg, J. H. *1931* (2).
Kelsey, F. D. — (1).
Leiberg, J. B. *2426* (1); *213*, *1064* (3); *227* (6); *227* (7).
Lemmon, J. G. — (6); — (10).
Letterman, G. W. *309* (1).
Lyall, D. *1680* (6).
Macbride, J. F. *961* (7).
MacDougal, D. T. *236* (1).
Mathias, M. E. *616* (12).
Mearns, E. A. *3242* (10).
Metcalfe, O. B. *411*, *1160* (1).
Minthorn, M. — (11).
Moore, Mrs. — (1).
Mulford, A. I. — (5); — (7).
Munz, P. A. *6830*, *6947*, *10640* (4).
Murdoch, J. *4098* (1).
Muir, J. *5024* (1).
Neally, G. C. *81* (1).
Nelson, A. *935*, *7516* (1).
Nelson, A. & E. *5629* (1).
Overholts, L. O. — (1).
Palmer, E. *304* (1); *229* (10); *305* (11).
Palmer, E. J. *31322* (1); *15132*, *17689*, *18075*, *25210* (2).
Pammel, L. H. *42* (1).
Parish, S. B. *10921* (4); —, *312*, *2415*, *7084* (10).
Parish, W. F. & S. B. —, *1474* (4); *1474* (6); *312* (10).
Parry, C. C. *310* (1); *203* (11).

Parry, C. C. & J. G. Lemmon, —, *232* (10).
Patterson, H. N. *243* (1).
Payson, E. B. & E. Bethel, *1153* (1).
Payson, E. B. & L. B. *1893* (1); *1796* (6a); *1796* (6b).
Peck, M. E. *4501* (6); *15174* (6a).
Piper, C. V. *1618* (3); *1619* (6a).
Pratt, A. D. — (1); *1618* (3), *1619* (6a).
Price, S. F. — (2).
Pringle, C. G. — (1).
Purpus, C. A. *304* (1); *1407* (8); — *3065* (11a).
Redfield, J. H. — (1).
Rose, J. P. *1624* (6).
Rothrock, J. T. *251* (1).
Rusby, H. H. — (11).
Russell). (2, C. —
Rydberg, P. A. & E. A. Bessey *4698* (1).
Sandberg, J. H. — (3); — (6a).
Sandberg, J. H., D. T. MacDougal & A. A. Heller *239* (3); *101* (6a).
Scribner, F. L. *156* (1).
Searls, Miss — (12).
Sheldon, E. P. *8344* (6a).
Small, J. K. — (2).
Smith, H. H. *405* (2).
Smith, L. E. *235* (6).
Snow, F. H. — (1).
Spalding — (3).
Standley, P. C. *4034* (1).
Starz, E. — (1).
Stokes, S. G. — (1).
Suksdorf, W. N. *938*, *939* (3); —, *40*, *161* (6); — (6a).
Thompson, J. W. *2851* (6a).
Tracy, J. P. *2244* (6).
Tracy, S. M. *1348* (2).
Trelease, W. — (1); *1130* (2).
Tuthill, F. H. *9* (2).
Vorhies, C. T. *43* (12).
Voth, H. R. *80* (12).
Watson, S. *270* (3).
White, J. *2* (10).
Wislizenus, F. *343* (2).
Wolf, J. — (1).
Woodson, R. E., Jr. & E. Anderson *29006* (11).
Young, A. H — (2).

INDEX TO SPECIES

New combinations are printed in **bold face** type; synonyms in *italics;* and previously published names in ordinary type.

	Page
Frasera	245, 256
albicaulis Dougl. ex Griseb.	246, 269
"*albicaulis* Griseb."	269
albicaulis f. *alba*	269
albomarginata	248, 249, 274
albomarginata var. **induta**	275
ampla	259
angustifolia	259
carolinensis	262
caroliniensis	245, 249, 251, 253, 254, 255, 258, 262
coerulea	253, 254, 255, 271
Cusickii	270
fastigiata	247, 248, 250, 251, 254, 255, 264
induta	275
macrophylla	259
montana	247, 266
neglecta	247, 255, 265
nitida	246, 247, 249, 250, 254, 267
nitida var. **albicaulis**	269
nitida var. *albida*	267
nitida var. **Cusickii**	270
officinalis	262
paniculata	246, 247, 248, 255, 275
Parryi	246, 248, 249, 255, 273
puberulenta	255, 272
speciosa	246, 247, 249, 250, 254, 255, 258
speciosa var. *angustifolia*	259
speciosa var. *scabra*	259
speciosa var. *stenosepala*	259

Page

stenosepala 259
thyrsiflora 246, 264
tubulosa 271
utahensis 275
venosa 259
verticillata 246, 262
Walteri 245, 262
Leucocraspedum 257
albicaule 269
albomarginatum 274
coeruleum 271
montanum 266
Mesadenia 246, 257
Sweertia 257
albicaulis 269
albomarginata 274
Bigelowii 275
carolinensis 262
fastigiata 264
Parryi 273

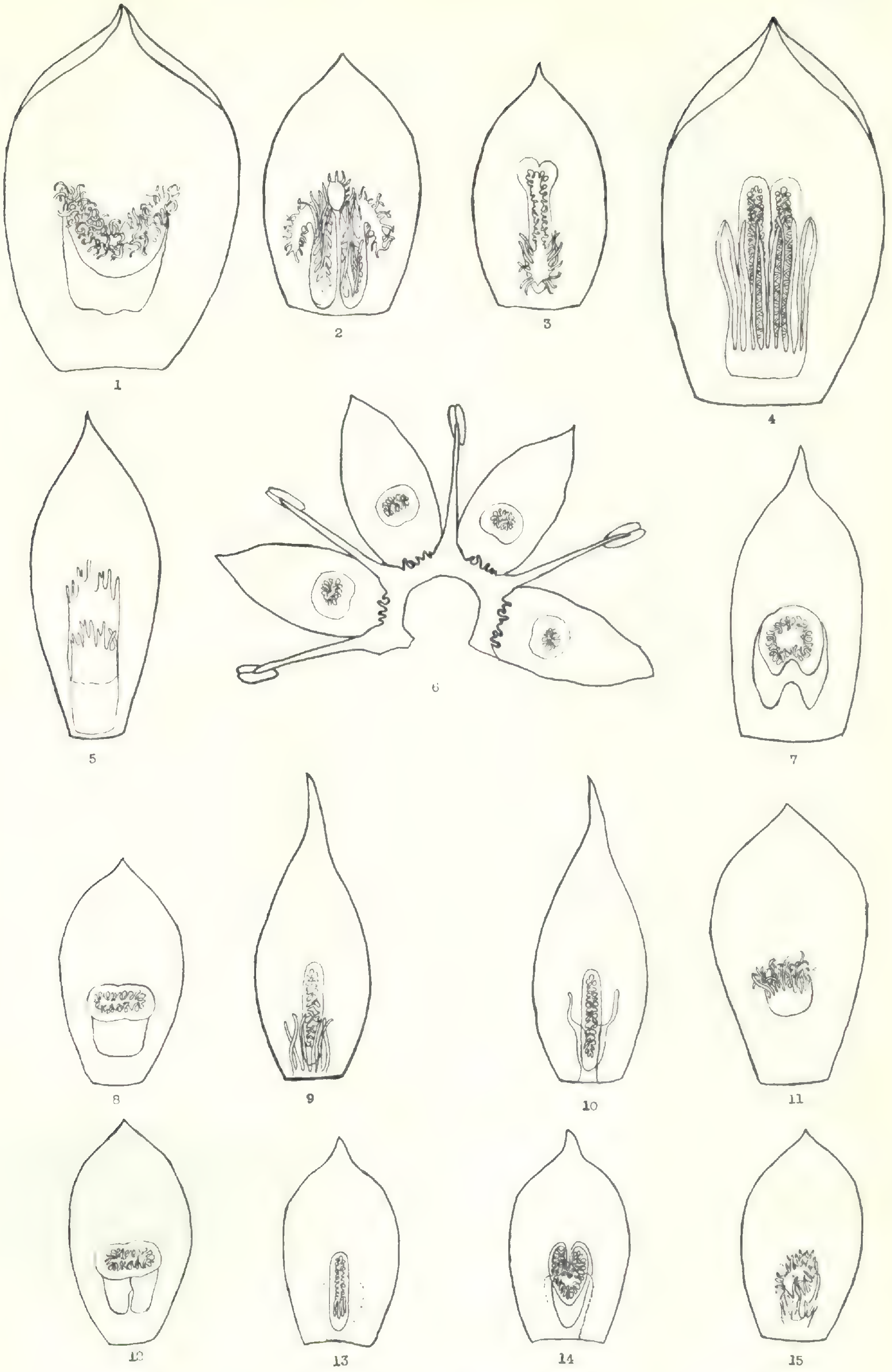
Page

radiata 259
Swertia 245, 247
Swertia 257
albomarginata 274
difformis 262
fastigiata 264
Frasera 262
neglecta 265
nitida 267
Parryi 273
tubulosa 271
Tessaranthium 257
angustifolium 259
macrophyllum 259
scabrum 259
speciosum 259
stenosepalum 259
Tesseranthium 246, 257
radiatum 259

Explanation of Plate

PLATE 14

Fig. 1. *F. Parryi.* Corolla-lobe and lunate fovea. × 6.
Fig. 2. *F. paniculata.* Corolla-lobe and foveae. × 6.
Fig. 3. *F. albomarginata.* Corolla-lobe and fovea. × 6.
Fig. 4. *F. speciosa.* Corolla-lobe, foveae and crown. × 6.
Fig. 5. *F. tubulosa.* Corolla-lobe and saccate fovea. × 6.
Fig. 6. *F. caroliniensis.* Corolla, stamens and reduced crown. × 6.
Fig. 7. *F. puberulenta.* Corolla-lobe and fovea. × 6.
Fig. 8. *F. neglecta.* Corolla-lobe and fovea. × 6.
Fig. 9. *F. nitida* var. *albicaulis.* Corolla-lobe, fovea and crown. × 6.
Fig. 10. *F. nitida* var. *Cusickii.* Corolla-lobe, fovea and petaloid crown. × 6.
Fig. 11. *F. fastigiata.* Corolla-lobe and fovea. × 6.
Fig. 12. *F. neglecta.* Corolla-lobe with partly fused foveae. × 6.
Fig. 13. *F. nitida.* Corolla-lobe, fovea, and crown. × 6.
Fig. 14. *F. nitida.* Corolla-lobe, foveae almost fused. × 6.
Fig. 15. *F. montana.* Corolla-lobe, fovea, and crown. × 6.



CARD—REVISION OF FRASERA

Explanation of Plate

PLATE 15

Fig. 1. Photograph of the type specimen of *Frasera nitida* Benth. var. *Cusickii* (Gray) Card, in the Gray Herbarium of Harvard University.

Fig. 2. Photograph of the type specimen of *Frasera puberulenta* Davidson, in the Herbarium of the Los Angeles Museum.

1

2

CARD—REVISION OF FRASERA

NOTES ON THE DISTRIBUTION OF SOME ROCKY MOUNTAIN PLANTS[1]

GEORGE J. GOODMAN

Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany of Washington University

A study of three collections of plants (Payson and Payson, 1926, and the writer's of 1927 and 1928) from the Uintah Mountains, Utah, revealed noteworthy extensions of the known ranges of a few species. These species, it will be noted, have their apparent centers of distribution in regions to the northwest and west of their newly discovered stations.

The Uintah Mountains, situated in the north-central part of Utah between the 40th and 41st parallels, extend from the Wahsatch range nearly eastward to northwestern Colorado, a distance of one hundred and twenty-five miles. They are the highest mountains in Utah, several of the peaks approximating 13,500 feet in altitude.

The foothills, which average about 8000 feet in altitude, are characterized by such typical regional plants as *Eriogonum heracleoides* Nutt., *Orthocarpus Tolmiei* H. & A., and the common Utah *Mertensia, M. Leonardi* Rydb. Large alpine meadows present a remarkably rich flora, and even such plants as *Parrya platycarpa* Rydb. and *Papaver alpinum* L. were found by the writer in plentifulness.

With the exception of the *Hesperochiron*, the collections of the following species are, so far as the writer knows, the only ones from Utah. These new localities extend eastward and southward the previously known geographical ranges of the species here recorded.

The Payson plants and the Goodman-Hitchcock specimen, cited below, are in various herbaria in this country. The Goodman plants are in his private collection, a nearly complete set of duplicates in the Rocky Mountain Herbarium, and the triplicates are in the Herbarium of Mr. George E. Osterhout, Windsor, Colorado.

[1] Issued June 30, 1931.

Arenaria cephaloidea Rydb. Bull. Torr. Bot. Club **39**: 316. 1912.

The specimen at hand agrees in all essential morphological characters with Rydberg's description.

UTAH: on dry rocky slopes, Uintah Mts., Summit Co., 8000 ft. alt., 29 July 1927, *Goodman 235*.

The previous known range is the submontane region of Washington and Idaho.

Lesquerella Kingii Wats. Proc. Am. Acad. **23**: 251. 1888.

UTAH: stony ridge on top of peak near West Fork of Bear River, Uintah Mts., Summit Co., 11,000 ft. alt., 7 July 1926, *E. B. & L. B. Payson 4901;* dry rocky soil, ridge east of East Fork of Bear River, Uintah Mts., about 11,000 ft. alt., 17 July 1928, *Goodman 528;* dry, gravelly soil, east of East Fork of Bear River, Uintah Mts., 10,500 ft. alt., 10 July 1930, *Goodman & Hitchcock 1505*.

Payson's *4901* was distributed as an unpublished variety of *Lesquerella prostrata* A. Nels.

In Payson's[2] monograph of the genus the distribution is given as "Nevada and southeastern California." Payson comments that "*Kingii* has not yet been collected in Utah. . ." The Utah collections extend the known range eastward about 375 miles.

Dodecatheon tetrandrum Suksdorf ex Greene, Erythea **3**: 40. 1895.

UTAH: meadows along margin of lake, east of Stillwater Fork, Uintah Mts., 10,100 ft. alt., 17 July 1926, *E. B. & L. B. Payson 5013;* margin of small lake, Uintah Mts., 10,500 ft. alt., 27 July 1927, *Goodman 220*.

The type of this species was collected in Washington, and the most southern or eastern stations heretofore known are western Nevada and Oregon. The Utah collections extend the range over 400 miles. The significance of this distribution can be more accurately evaluated after the status of the species is better known.

Hesperochiron pumilus (Griseb.) Porter in Hayden, Rept. Geol. Surv. 778. 1873; Brewer & Watson, Bot. Calif. **1**: 517. 1876; Gray, Syn. Fl. N. A. **2**[1]: 173. 1878; Jepson, Man. Fl. Pl. Calif. 835. 1925.

[2] Payson, E. B., Monograph of Lesquerella. Ann. Mo. Bot. Gard. **8**: pp. 216–217. 1921.

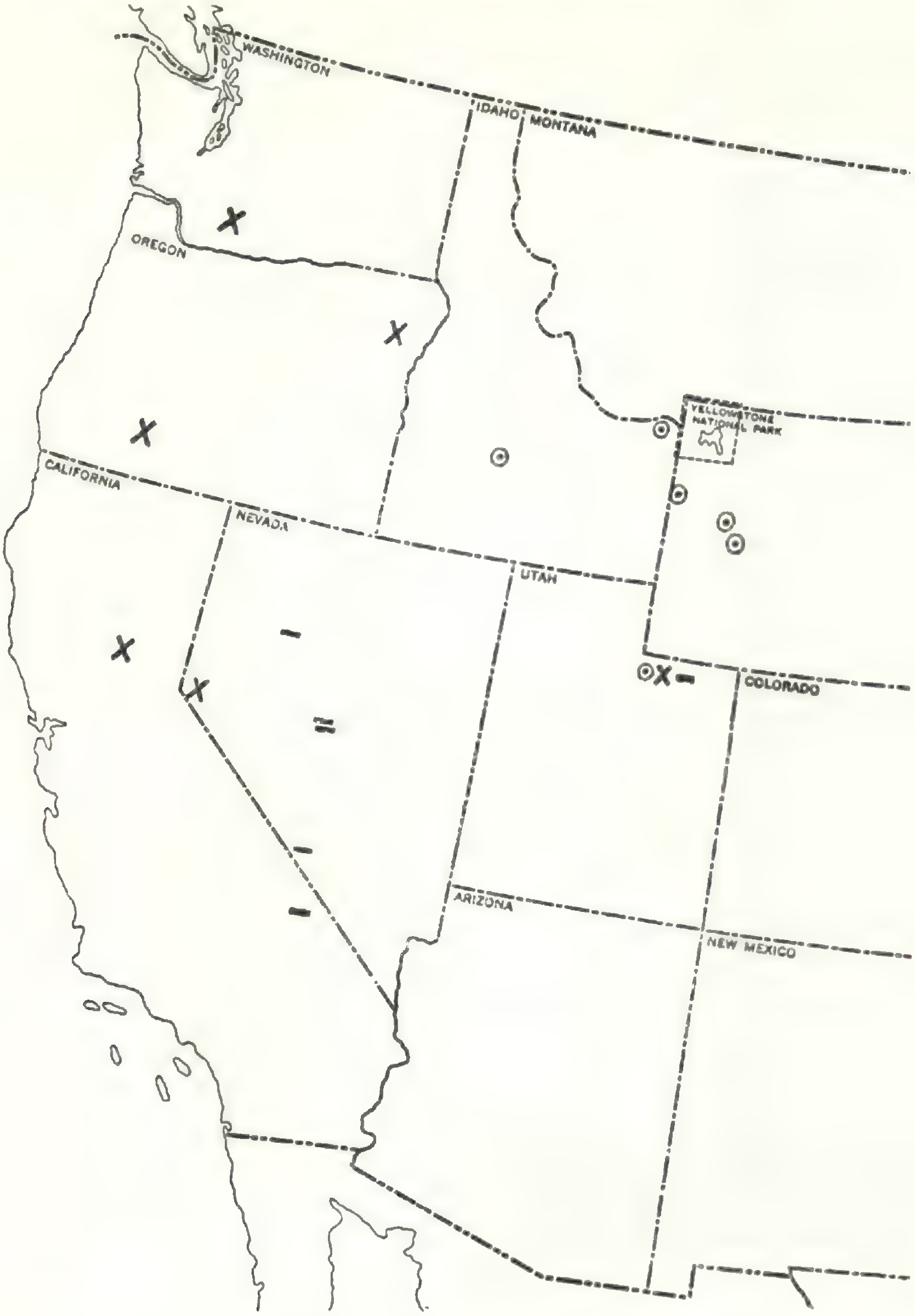


Fig. 1. Map of the western United States, showing the distribution of three species of plants.

Lesquerella Kingii .... ▬

Dodecatheon tetrandrum .... ✕

Mertensia incongruens .... ⊙

Villarsia pumila Griseb. in Hook. Fl. Bor.-Am. **2:** 70, *pl. 157 B.* 1838; Griseb. Gen. et Sp. Gent. 338. 1839.

Capnorea pumila Greene, Erythea **2:** 193. 1894; Tidestrom in Contr. U. S. Nat. Herb. **25:** 449. 1925.

In accepting the generic name *Hesperochiron*, accordance is made with the list of Nomina Conservanda in the International Rules of Botanical Nomenclature (1906).

Utah: moist soil near West Fork of Bear River, Uintah Mts., 9800 ft. alt., 7 July 1926, *E. B. & L. B. Payson 4925;* in damp sod, foothills of Uintah Mts., 7900 ft. alt., 26 June 1928, *Goodman 401.*

Most of the herbarium specimens examined are from Idaho, Washington, Oregon, and Montana. One specimen, collected by Aven Nelson, is from Evanston, Wyoming, only a short distance from the Utah station.

Mertensia incongruens Macbr. & Payson, Contr. Gray Herb N. S. 49: 66. 1917.

Utah: rocky slope, Uintah Mts., 11,300 ft. alt., 30 July 1927, *Goodman 257.*

The type of this species was collected in Blaine County, Idaho. Collections since then (excepting the specimen cited above), as represented in the herbarium of the Missouri Botanical Garden and the Rocky Mountain Herbarium, have all been collected by the Paysons and are from Idaho, Teton Pass, Wyoming, or Sublette County in west-central Wyoming.

The range for this species is thus extended southward about 175 miles.

The writer wishes to thank Dr. Aven Nelson, Curator of the Rocky Mountain Herbarium, for having checked over a few specimens at that institution, and Dr. J. M. Greenman, who has characteristically aided generously and critically.

Annals of the Missouri Botanical Garden

Vol. 18 SEPTEMBER, 1931 No. 3

THE POLYPORACEAE OF COLORADO[1]

PAUL FRANKLIN SHOPE

Assistant Professor, Department of Biology, University of Colorado
Formerly Missouri Botanical Garden Special Fellow in Botany

I. Introduction

SCOPE AND AIM

The purpose of this paper is to give a detailed account of the different members of the Polyporaceae found in Colorado. This account includes all the pore fungi known to occur in the state up to the time of publication. Yet at the rate in which species new for this region have been found during the past years it is evidently not all-inclusive. The state is so large and some regions so inaccessible that an exhaustive survey of this region for pore fungi could not be completed in a lifetime by any one individual. At all events, this treatise includes all members of the family which are frequently encountered.

A consideration of the Polyporaceae has a two-fold aspect: the first is the purely taxonomic aspect of the subject with which this paper primarily deals; the second is the economic phase of the subject, which is only suggested in this study. The pore fungi are of great economic importance in the decay of both living and dead trees, structural timber, fence posts, telephone poles, railroad ties, and all other things made of wood.[2] In addition to the pore fungi, other families of fungi, such as the Hydnaceae, the Thelephoraceae, the Agaricaceae, etc., are responsible in rendering merchantable timber worthless.

[1] An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

[2] Hubert, E. E. Outline of forest pathology. New York, 1931.

Issued October 28, 1931.

Only one member of the Polyporaceae is known to enter into a mycorrhizal relation with the roots of forest trees. Masui[3] reports that *Polyporus leucomelas* forms such a relation with *Pinus densiflora*.

Although this paper deals particularly with the Colorado polypores, it is more or less adaptable to the entire Rocky Mountain range, due to the fact that the trees upon which these fungi grow and with which they are for the greater part coextensive are usually distributed throughout that region. For example, Douglas spruce (*Pseudotsuga mucronata*) reaches its best development in Colorado, but extends far north and south. Lodgepole pine (*Pinus Murrayana*) is found throughout the Rocky Mountains and even in Alaska, as well as in California. In the use of this treatise in states other than Colorado, it is to be remembered that timberline in Colorado is about 11,500 feet; whereas in more northern regions it occurs at a lower elevation (9,000 feet in Montana; 7,000 feet in Alberta), and is higher southwards. On the western slope in the Rocky Mountains, any particular tree-species is 1,000 feet lower in elevation than the same species on the eastern slope.

HISTORY

Up to the present time, nearly all the information on Colorado fungi has been gathered by out-of-state collectors who have visited Colorado for one or more summers, as: J. C. Arthur, F. D. Kern, Fred J. Seaver, L. O. Overholts, C. H. Kauffman, E. Bartholomew, C. L. Shear, and others. Within the state there has been only one noteworthy collector of fungi who was more interested in the rusts on conifers than in any other branch of mycological work. He was the late Ellsworth Bethel, who collected in Colorado from 1894 to 1925, which latter date marked his untimely death. Mention should be made also of the work of W. C. Sturgis on the slime molds. A more detailed account of the history of mycological collectors in Colorado may be found elsewhere.[4]

[3] Masui, K. A study of the ectotrophic mycorrhizas of woody plants. Kyoto Imp. Univ. Mem. Coll. Sci. **3B**: 179. 1927.

[4] Shope, P. F. History of mycological collectors in Colorado. Mycologia **21**: 292–296. 1929.

II. Distribution

GENERAL CONSIDERATION

Since pore fungi are for the greater part either parasitic or saprophytic on wood, the general opinion has prevailed that their distribution is primarily coextensive with that of their hosts. Ramsbottom[5] states: "No attempt to understand the ecology of the larger fungi can be successful unless they are considered in their relation to higher plants, for, in addition to edaphic factors, light, heat, moisture and movement of the atmosphere play a a part." Rea[6] has somewhat the same idea; he states: "The problem of the distribution of the British macrofungi is based on their association with other plants. This association is either saprophytic, parasitic, or symbiotic, but the majority of the macrofungi belong to the first group. Other factors governing the distribution of the larger fungi are the geological formation and nature of the soil on which they grow, the humidity or dryness of the atmosphere or habitat, the height above sea level, the density of growth and the presence or absence of strong light especially in woods."

Before entering into the discussion of the distribution of the pore fungi of Colorado, it would be well to consider the zones of vegetation for the higher plants of this region. Ramaley's[7, 8] divisions of the plant zones for the Rocky Mountains of Colorado will be used in this paper. A synopsis of the general characteristics, as well as a list of the higher plants and fungi which occur in these zones, will follow. The altitude for each of these zones is given in relation to vegetation on eastern slopes in central Colorado. Changes should be made in elevations for regions north and south as well as for western slopes.

1. *Plains zone:* up to 6,000 feet. Mean annual temperature 49.8° F. Annual precipitation 14.2 inches; 5 feet of snow.[9] Meso-

[5] Ramsbottom, J. in Tansley, A. G. & T. F. Chipp. Aims and methods in the study of vegetation. p. 162. London, 1926.

[6] Rea, C. The distribution of the dominant British macrofungi. Paper presented before the International Congress of Plant Sciences. Ithaca, N. Y. 1926. Quotation from author's abstract.

[7] Ramaley, F. R. Plant zones in the Rocky Mountains of Colorado. Science, N. S. **26**: 642–643. 1907.

[8] ————, Colorado plant life. pp. 3–6. Boulder, 1927.

[9] ————, & G. S. Dodds, The University of Colorado Mountain laboratory at Tolland, Colorado. Univ. Colo. Studies **12**: 8. 1917.

phytic in the spring due to the accumulation of moisture in the soil from the winter's melting snow and also the spring rains. After the spring rains this region is for the greater part arid. In general, the vegetation of the region is that of dry grassland with an abundance of spring-blooming herbs. Cottonwoods (*Populus* spp.) and willows (*Salix* spp.) are found bordering the streams; a few pines (*Pinus* spp.) and junipers (*Juniperus* spp.) occupy exposed sandy bluffs. Sagebrush (*Artemisia* spp.) and rabbit-brush (*Chrysothamnus* spp.) are sometimes intermixed with the grasses. The soil is fine-grained alluvium, sometimes covered with wind-blown deposits.

Polyporus versicolor, *P. adustus*, and *Trametes hispida* are found abundantly on willows (*Salix* spp.) and cottonwoods (*Populus* spp.). In the spring and during the short moist season many gill fungi abound. Puffballs are found in the grasslands, but all disappear on the advent of dry soil conditions in late spring. Many rusts occur on different members of the *Poaceae* and on various species of *Artemisia*. These rusts persist throughout the summer and autumn.

2. Foothill zone: 6,000 to 8,000 feet. This zone is slightly better watered than the plains zone. Summer showers occur frequently in the hills but seldom reach the plains; and in winter many a light snowfall in the mountain does not extend down below the foothills. In this zone, the snow that falls during the winter is entirely melted by the early part of May. The characteristic vegetation is open forests of rock pine (*Pinus scopulorum*) with an intermixing of Douglas spruce (*Pseudotsuga mucronata*) and junipers (*Juniperus* spp.). Pinyon pine (*Pinus edulis*) occurs south of Colorado Springs and in scattered areas north of Fort Collins, Colorado. Chaparral of oak (*Quercus* spp.), mountain mahogany (*Cercocarpus* spp.), and other shrubby xerophytic plants is found, especially in the southern part of the state. Cottonwoods (*Populus* spp.) and willows (*Salix* spp.) of various kinds, aspen (*Populus tremuloides*), maple (*Acer glabra*), birch (*Betula* spp.), mountain ash (*Sorbus scopulina*), thorn-apple (*Crataegus* spp.), sumac (*Rhus cismontana*), and others represent the woody deciduous vegetation. The soil is somewhat more gravelly than that of the plains.

Polyporus versicolor, *P. adustus*, and *Trametes hispida* occur on willows (*Salix* spp.), cottonwoods (*Populus* spp.), and aspen (*Populus tremuloides*). Rock pine (*Pinus scopulorum*) and Douglas spruce (*Pseudotsuga mucronata*) harbor *Trametes odorata* (*T. protracta* in the American sense), *Polyporus abietinus*, *Lenzites saepiaria*, *Trametes subrosea*, *Fomes Pini*, and *F. pinicola*. *Polyporus volvatus* has been found a few times on rock pine (*Pinus scopulorum*) in this region.

3. *Montane zone:* 8,000 to 10,000 feet. Mean annual temperature 41.0° F. Annual precipitation 24.16 inches; 15 feet of snow. In this zone and above the rainfall and snowfall are considerable. During the summer months showers of short duration occur almost daily; at times there are long-continued rains. The snowfall is heavier than in the foothill zone, and snowdrifts, sheltered under the trees, persist until June or July. Due to a late spring and an early autumn in this region, the growing season is from three to three and one-half months. Here are coniferous forests of lodgepole pine (*Pinus Murrayana*), or lodgepole pine mixed with Engelmann spruce (*Picea Engelmanni*), Douglas spruce (*Pseudotsuga mucronata*), and rock pine (*Pinus scopulorum*). This zone represents the uppermost limit for Douglas spruce (*Pseudotsuga mucronata*), rock pine (*Pinus scopulorum*), pinyon pine (*Pinus edulis*), concolor fir (*Abies concolor*), and all the junipers (*Juniperus* spp.) with the possible exception of *Juniperus sibirica*, which sometimes extends up into the subalpine zone. The Colorado blue spruce (*Picea pungens*), with a range of 7,000 to 9,000 feet on the eastern slope, and a range of 6,000 to 8,000 feet on the western slope, reaches its best development in the lower altitudes of this zone and in the upper foothill zone. It is found only in moist locations and usually bordering on streams. Aspens (*Populus tremuloides*) are best developed and form dense groves in this zone, but their altitudinal distribution is greater than that of any other tree in Colorado. Aspens may be found in the foothills and extending up through the different zones almost to timberline. Mountain parks represent a conspicuous part of the landscape in this zone and extend up into the lower limits of the subalpine zone. Different species of cottonwoods (*Populus* spp.) and willows (*Salix* spp.), alder (*Alnus tenuifolia*),

elder (*Sambucus* spp.), birch (*Betula* spp.), mountain maple (*Acer glabrum*), hazelnut (*Corylus rostrata*), choke cherry (*Prunus melanocarpa*), and wild cherry (*Prunus americana*) represent the woody deciduous plants in this zone.

The montane and subalpine zones furnish the best collecting grounds in the state. The common pore fungi found mainly on coniferous hosts are: *Fomes Pini*, *F. pinicola*, *Polyporus alboluteus*, *P. leucospongia*, *P. abietinus*, *P. ursinus*, *Trametes variiformis*, *T. isabellina*, *T. odorata*, and *Lenzites saepiaria*. Those found on deciduous hosts are: *Fomes igniarius* and *Polyporus adustus*. Many gill fungi abound in the well-wooded areas. Rusts are found on grasses and conifers. There are many thelephoraceous species, of which *Stereum rugisporum* is very common. *Auricularia Auricula-Judae* (Jew's ear fungus), *Dacryomyces abietinus*, *Exidia glandulosa*, *Guepinia monticola* and other jelly-like species are of frequent occurrence here as well as in the subalpine zone. Cup fungi are well represented; *Dasyscypha Agassizii* and *D. arida* are both common.

4. Subalpine zone: 10,000 to 11,500 feet. The mean annual temperature in this zone is a few degrees cooler than that of the montane zone; also, there is slightly more rain in the summer and more snow during the winter than in the lower adjacent zones. Snowdrifts often remain in the closed stands of Engelmann spruce (*Picea Engelmanni*) until August. Again, the snow which has accumulated during the winter may not entirely disappear during the few warm months of the summer. The growing season is from two and one-half to three and one-half months. The upper limit of this zone is characterized by dwarfed timberline trees of Engelmann spruce (*Picea Engelmanni*), sometimes mixed with bristle-cone pine (*Pinus aristata*), lodgepole pine (*Pinus Murrayana*), and subalpine fir (*Abies lasiocarpa*). The floor of the Engelmann spruce forest is usually covered with a mat of blueberry plants (*Vaccinium* spp.). The woody deciduous plants of common occurrence are dwarf willow (*Salix* spp.) and aspen (*Populus tremuloides*).

Nearly all the fungi found on conifers in the montane zone extend up into the lower limits of this zone. Deciduous trees and shrubs are sparse in this region. *Polyporus leucospongia*, *P. albo-*

luteus, and *Lenzites saepiaria* are the dominant pore fungi near timberline. *Vaccinium oreophilum* is often badly infected with the rust fungus *Calyptospora columnaris*. Rusts on coniferous trees, gill fungi, and cup fungi are frequently found. *Paxina nigrella*, growing a short distance from the edge of snowdrifts, is of interest because of its habitat.

5. *Alpine zone:* above 11,500 feet, or above timberline. Mean annual temperature 26.0° F. Annual precipitation 43.69 inches, most of which falls in the form of snow. The growing season is very short, only two to two and one-half months. No trees are present, but low thickets of dwarf willow (*Salix* spp.) are found in protected places. Above timberline, there are grassland steppe or tundra and rock desert, and in all of these formations the soil is coarse and gravelly. Many herbaceous plants are mat- or cushion-like and all assume a low or prostrate growth-form. Rather limited areas of grasses and sedges exist.

Due to the absence of trees and to the dryness of the soil, this region contains very few fungi and no polypores. A few gill fungi, some cup fungi, and rust fungi represent the sparse mycological flora.

These plant zones intergrade one into the other. There is no abrupt change in vegetation as one passes from the altitudinal boundary of one zone into the next. However, the plants observed at the altitudinal middle-distance of one zone will be found to be markedly different from those observed from a similar position in an adjacent zone. The characteristic vegetation of any zone is not drawn from the plants found near the altitudinal limits of that zone, but from the plants found in its altitudinal middle-distance.

The differences in plant life, as one proceeds from a lower to a higher elevation, are correlated primarily with differences in climate. Contrasting the alpine zone with lower zones, the following climatic and edaphic factors may be listed for the higher zone, as follows:

Colder air temperature.
More rare atmosphere.
Brighter sun.
Shorter growing season.

Higher winds.
Coarser soil.
Colder soil.
Lower relative humidity.
Dryer soil due to rapid evaporation; or else physiologically dry soil due to frost or low soil temperature.
More precipitation, most of which falls in the form of snow.
Possible difference in the soil reaction, in chemical constituents, and in the micro-flora and -fauna of the soil.

In the consideration of the distribution of the fungous flora of these different zones, only the more common species have been listed in the zones where they seem to be most abundant. An overlapping of species occurs in adjacent zones, but, as with certain trees which are dominant in a particular zone, some fungi belong primarily and are of more common occurrence in a certain zone.

Summarizing the preceding data on the zonal distribution of pore fungi, the more sparse flora occurs in the plains zone, the lower limits of the foothill zone, the upper limits of the subalpine zone, *i. e.*, timberline and the alpine zone. In other words, the two altitudinal extremes contain few fungi, whereas the regions between these limits contain many more. Many species are confined to a single zone or to two adjacent zones, others are widespread in their distribution. It is clear from the foregoing paragraphs that there is a distinct correlation between the abundance of woody plants in a region and the occurrence of pore fungi.

Since both common and scientific names[10] are used for the host plants in this treatise, a list of the more common trees with their synonyms and altitudinal range will follow. The first scientific name is the accepted one; those following are synonyms. Where two or more common names are given, the first one is generally used throughout this work.

Coniferous plants:

Abies concolor Lindl. & Gord. Concolor Fir, White Fir. 8,000–10,000 feet.

[10] The classification used for the phanerogams is based primarily on Coulter, J. M. & A. Nelson's 'New manual of Rocky Mountain botany.' New York, 1909.

Abies lasiocarpa (Hook.) Nutt. (*Pinus lasiocarpa* Hook.; *Abies subalpina* Engelm.). Subalpine Fir, Alpine Fir, Balsam. 8,000–11,500 feet.

Juniperus communis L. Low Juniper. 5,000–8,000 feet.

Juniperus monosperma (Engelm.) Sarg. (*Sabina monosperma* (Engelm.) Rydb.; *Juniperus occidentalis monosperma* Engelm.). One-seeded Juniper. 5,000–7,000 feet.

Juniperus scopulorum Sarg. (*Sabina scopulorum* (Sarg.) Rydb.). Red Cedar, Rocky Mountain Red Cedar. 4,500–8,500 feet.

Juniperus sibirica Burgsd. Mountain Juniper, Low Juniper. 6,000–10,000 feet.

Juniperus utahensis (Engelm.) Lemm. (*Sabina utahensis* (Engelm.) Rydb.). Utah Juniper, Desert Juniper. 6,000–9,000 feet.

Picea Engelmanni or *P. Engelmannii* (Parry) Engelm. (*Abies Engelmanni* Parry; *Picea columbiana* Lemm.). Engelmann Spruce. 8,500–11,500 feet.

Picea pungens Engelm. (*Picea Parryana* (Andre) Sarg.; *Abies Menziesii Parryana* Andre). Colorado Blue Spruce. 6,500–10,500 feet.

Pinus aristata Engelm. Bristle-cone Pine, Foxtail Pine. 8,500–11,500 feet.

Pinus edulis Engelm. (*Caryopitys edulis* (Engelm.) Small). Pinyon Pine. 4,000–9,000 feet.

Pinus flexilis James (*Apinus flexilis* (James) Rydb.). Limber pine. 7,500–11,000 feet.

Pinus Murrayana Balf. (*Pinus contorta* Loudon). Lodgepole Pine. 6,500–10,500 feet.

Pinus scopulorum (Engelm.) Lemm. (*Pinus ponderosa scopulorum* Engelm.). Rock Pine, Yellow Pine. 5,000–9,000 feet.

Pseudotsuga mucronata (Raf.) Sudw. (*Pseudotsuga taxifolia* (Lamb.) Britt.; *P. Douglasii* (Lindl.) Carr.; *Abies mucronata* Raf.; *Pinus taxifolia* Lamb.). Douglas Spruce, Douglas Fir. 6,000–10,000 feet.

Deciduous plants:

Acer glabrum Torr. (*Acer neomexicanum* Greene). Rocky Mountain Maple. 5,000–9,000 feet.

Acer Negundo L. (*Negundo aceroides* Moench; *Negundo Negundo* (L.) Karst.; *Rulac Negundo* Rydb.; *Rulac texanum* Rydb.). Box Elder. 5,000–6,500 feet.

Alnus tenuifolia Nutt. (*Alnus incana virescens* S. Wats.). Alder. 5,000–10,000 feet.

Betula fontinalis Sarg. (*Betula occidentalis* Nutt.). Canyon Birch, Fountain Birch, Rocky Mountain Bog Birch. 5,000–9,000 feet.

Betula glandulosa Michx. Scrub Birch, Swamp Birch. 8,500–11,000 feet.

Corylus rostrata Ait. Hazel-nut. 5,500–8,000 feet.

Crataegus spp. Thorn-apple, Hawthorn. Probably five species, with a range of 5,500–7,000 feet.

Populus angustifolia James. Narrow-leaf Cottonwood. 5,000–9,000 feet.

Populus occidentalis (Rydb.) Britt. (*Populus deltoides occidentalis* Rydb.; *P. angulata* Port. & Coult.; *P. Sargentii* Dode). Cottonwood, Western Cottonwood. 5,000–9,000 feet.

Populus tremuloides Michx. Aspen, Trembling Aspen, Quaking Aspen. 5,800–10,000 feet or more.

Prunus americana Marsh. Wild Plum. 5,000–8,000 feet.

Prunus melanocarpa (A. Nels.) Rydb. (*Prunus demissa* Torr. in part; *Cerasus demissa melanocarpa* A. Nels.). Choke Cherry. 5,000–9,000 feet.

Prunus pennsylvanica L. f. Wild Cherry. 6,000–9,000 feet.

Rhus cismontana Greene (*Rhus glabra* L.; *R. nitens*, *R. tessellata*, *R. albida*, and *R. asplenifolia* Greene). Sumac. 5,500–7,500 feet.

Salix spp. Willow. Probably twenty-eight species, with a range of 5,500–14,000 feet.

Shepherdia argentea Nutt. (*Lepargyaea argentea* (Nutt.) Greene). Buffalo Berry, Bull-berry. 5,000–6,000 feet.

Sorbus scopulina Greene. Mountain Ash. 6,000–10,000 feet.

Ulmus americana L. American Elm, White Elm. Introduced. 5,000–5,500 feet.

FACTORS DETERMINING THE DISTRIBUTION OF THE POLYPORACEAE

The geographic and climatic factors which are responsible for the distribution of fungi in this region are listed as follows:

Topography of the country.

Temperature and its influence upon spore germination and growth.

Physical and chemical nature of the substratum.

Moisture and its influence upon spore germination and growth.

Topography of the country.—Northern slopes when compared with southern ones of a similar elevation are more moist throughout the spring and early summer due to the slower melting of the winter's accumulated snow; thus they support a richer flora of both fungi and higher plants. Likewise, western slopes when compared with eastern ones are favored with better moisture conditions. Areas protected from prevailing winds are more moist and harbor a richer fungous flora than exposed slopes. Regions bordering on streams and lakes are usually well watered.

Specimens of pore fungi under alpine conditions usually differ from the same species found at lower levels by their smaller size and their tendency towards resupinate growth. This is well shown in *Polyporus abietinus* and *Fomes Pini*, which are most often found to be resupinate at their highest points of distribution. In dry locations and also in high altitudes, sporophores are usually found closer to the ground than in more moist or lower situations.

Temperature and its influence upon spore germination and growth.—Snell[11] shows that there is an optimum temperature for spore germination which is different for different species. Furthermore, he shows that these temperatures may not be the same as the optimum temperature for the best mycelial growth of the species. If new infections originate from germinating spores, this may result in the limitation of a species to a zone where a favorable temperature for spore germination prevails during that period. However, indications point to the fact that the inocula for many primary infections come from the soil. Snell[12] reports that the spores of *Lenzites saepiaria* germinate at temperatures ranging from 12° C. to 40° C., and those of *Trametes serialis* from 3° C. to 40° C. He shows that at these temperature extremes, the spores require a relatively long time for germination, in some cases as long as two days. Furthermore, he points out that in

[11] Snell, W. H. Studies of certain fungi of economic importance in the decay of building timber. U. S. Dept. Agr., Bull. 1053. 1922.

[12] ———, *l. c.* p. 8.

most of the species with which he worked, the greater percentage of spore germination and the most rapid growth take place at temperatures from 28° to 32° C.

Although temperatures from 28° to 32° C. are rarely reached in the plains and foothills zones, and probably never at higher elevations, there are days throughout the growing period when relatively favorable temperatures for spore germination do exist; but during the night, at high elevations, the temperature may fall to near 0° C. Since, as pointed out by Snell (*l. c.*), it takes from twenty hours to several days for spores of the pore fungi to germinate *in vitro*, even under the most favorable conditions of moisture and temperature, favorable conditions during the daytime apparently do not represent a sufficient length of time for germination. The actual effect of the cold nights upon spore germination of the pore fungi is unknown to the writer, but it is thought that the cold nights only retard germination and growth of the germ-tube. Thus the germination period is lengthened as a result of the alternate favorable and unfavorable conditions of temperature. Moreover, even though there is a pronounced change in the day and night air temperatures, during the night the temperature of the substrata and soil does not change as rapidly nor to the same extent as that of the air. Hence spores which are deposited upon a substratum may not be subjected to the same nightly drop in temperature as that of the air. Barring the possibility that all primary infections at higher elevations come from inocula in the soil which originally attained these higher elevations by the slow process of vegetative migration from lower levels where conditions for spore germination were more favorable, or else conveyed by animals or birds, the presence of the pore fungi under these conditions would indicate that spore germination actually takes place, resulting in infection.

The arctic conditions of the higher regions during the winter months evidently do not kill pore fungi. Buller and Cameron[13] have demonstrated that the fruiting bodies of several pore fungi can withstand temperatures of −100° C. or lower. Certainly no such extreme in temperature exists in the Rocky Mountains.

[13] Buller, A. H. R. & A. T. Cameron. On the temporary suspension of vitality in the fruit bodies of certain Hymenomycetes. Trans. Roy. Soc. Can. III. 6: sect. 4, 73–75. 1912.

Miss Stevens[14] has pointed out that: ". . . at night or in the shade the temperature of twigs and small branches approximate that of the air, whereas in the sunlight their temperature is generally above, sometimes as much as 20° C. above that of the air." This datum is of importance in the growth of fungi which are already established, but as far as spore germination is concerned the direct rays of the sun probably do more damage in drying out the substratum than they do good in giving heat to the germinating spores. In this connection, the possible harmful effects of ultra-violet at high elevations should not be overlooked.

Since the wealth of our fungous flora is primarily limited to the heavily forested regions where the sun's rays seldom penetrate to the forest floor, heat from the direct rays of the sun plays a minor role. It has been noted,[15] however, that pore fungi are of a darker color at high elevations, thus possessing a greater ability to absorb heat. A departure from this is *Polyporus leucospongia* which is frequently found growing in exposed places. This fungus is of a whitish color which may be instrumental in reducing the quantity of heat absorbed from the sun's intense rays at high elevations, thus lowering the rate of evaporation.

Physical and chemical nature of the substratum.—Weir[16] states that: "Any factor that influences the cellular and chemical development of the wood of a tree may influence the growth of some wood-destroying fungi, hence their distribution. Aside from the moisture relation which is always a factor in promoting the growth of fungi, the influence of elevation on the chemical and anatomical structure of forest trees is a well known phenomenon and in a measure determines their predisposition to disease."

The writer[17] has elsewhere pointed out the anatomical changes in aspen at different elevations in Colorado. Trees growing at high elevations have narrower annual increments of growth, and in many cases, harder wood than the same species found at lower

[14] Stevens, N. E. Environmental temperatures of fungi in nature. Am. Jour. Bot. **9**: 286. 1922.

[15] Weir, J. R. Notes on the altitudinal range of forest fungi. Mycologia **10**: 4–14. 1918.

[16] ———, *l. c.* p. 8.

[17] Shope, P. F. Stem and leaf structure of aspen at different altitudes in Colorado. Am. Jour. Bot. **14**: 116–119. 1927.

levels. This, according to Zeller,[18] makes the high altitude trees more resistant to decay through the reduction of the volume of air content of the wood. Other anatomical features, such as size of cells, thickness of cork, and proportions of spring and summer wood, probably play a more or less important role in the predisposition of the host to disease. The quantity and distribution of resin, tannin, gums, and lignin are factors for additional consideration.

As to the soil as a substratum for pore fungi, there is a change in the quantity, quality, and physical and chemical make-up of soils at different elevations. Very little data are at hand on this phase of the subject; however, few pore fungi in this region are ground-inhabiting.

Moisture and its influence upon spore germination and growth.—With reference to spore germination, temperature relations have already been considered under the second heading; moisture relations, however, have yet to be considered. Zeller[19] has shown that the best rate of germination of spores of *Lenzites saepiaria* on wood takes place when the moisture of the substratum is at or in excess of the fiber saturation point, and at a lower moisture content the rate and percentage of germination are relatively lower. A condition of moisture adequate to produce the fiber saturation point of the substrata would exist at timberline only during the spring of the year when the snow is melting. In the lower subalpine and in the upper montane zones, such conditions would exist well into the summer and in some years during the entire growing season. In the foothill and plains zones, these conditions of moisture would exist only during the spring and early summer, or during unusually wet summers. Indications would point to the fact that infection from the germination of spores takes place mainly during these periods of suitable moisture conditions.

If conditions for spore germination are favorable during certain parts of the year at all elevations, it may be assumed that during these same seasons of the year, conditions would be favorable for

[18] Zeller, S. M. Physical properties of wood in relation to decay induced by *Lenzites saepiaria*. Ann. Mo. Bot. Gard. 4: 93–164. 1917.

[19] ———, Humidity in relation to moisture imbibition by wood and to spore germination on wood. Ann. Mo. Bot. Gard. 7: 68–74. 1920.

mycelial growth and sporophore production. However, the accumulated snow, in most cases, has disappeared by July or August and the soil and substrata slowly dry out to be watered throughout the remainder of the season only by occasional showers of short duration. The question is, how do these fungi persist through the summer or dry season?

The great amount of precipitation in the subalpine and montane zones would indicate a luxuriant growth of all kinds of vegetation. As previously mentioned, fungi are most abundant in these zones, but these same zones may become quite arid during the months of July, August, and September, especially as timberline is approached. The dryness of the timberline region is not due to lack of precipitation, but to drainage and the exceedingly rapid rate of evaporation induced by high winds and low humidity. The plains are likewise arid during the summer months, because rainfall is very much less than at higher elevations and a great part of the precipitation falls during the non-growing seasons of the year. The problem, then, is to account for the presence of pore fungi at timberline and in the lower foothill and plains zones. The pore fungi at timberline will be considered first.

TABLE I

PERCENTAGE OF WATER ABSORPTION, BASED ON PERCENTAGE AIR-DRY WEIGHT

	Intervals in minutes					
	10	20	30	40	50	60
Polyporus versicolor	192.8	215.4	226.2	233.3	238.1	238.1
Trametes hispida	210.3	227.8	244.3	258.7	263.9	271.0
Polyporus adustus	315.2	325.0	328.1	329.3	331.2	335.0
Trametes odorata	177.8	181.1	188.2	190.5	196.0	197.5
Trametes subrosea	180.3	195.0	195.0	195.0	195.9	195.9
Fomes Pini	55.3	73.7	87.7	99.5	109.0	118.4#
Fomes pinicola	59.4	93.9	108.4	113.9	116.3	116.6#
Lenzites saepiaria	250.4	264.7	271.7	274.6	277.5	284.1
Polyporus leucospongia	483.6	523.6	603.5	619.3	636.7	650.0
Polyporus ursinus	130.9	165.7	183.0	194.1	205.5	207.6
Polyporus alboluteus	465.5	540.8	556.3	583.5	587.3	589.8

All specimens were saturated at the end of one hour's soaking, except those marked "#."

TABLE II

PERCENTAGE OF WATER LOSS THROUGH EVAPORATION, BASED ON PERCENTAGE SATURATED WEIGHT

	Intervals in hours															
	4	6	10	16	20	24	28	41	46	50	65	91	103	150	180	220
Polyporus versicolor	52.8	70.7	90.0	100												
Trametes hispida	25.2	37.1	65.2	75.0	84.9	91.5	97.5	100(32 hrs.)								
Polyporus adustus	24.8	36.2	70.5	88.5	91.6	97.0	100									
Trametes odorata	20.1	29.2	57.5	68.0	78.6	86.2	93.6	99.5	100							
Trametes subrosea	10.9	24.3	54.5	66.8	75.6	82.6	90.0	98.8	100							
Fomes Pini	8.2	14.6	16.2	30.0	38.8	50.5	55.3	62.8	68.8	73.5	80.0	88.6	92.5	99.0	100	
Fomes pinicola	6.7	11.8	12.7	25.4	32.4	37.6	43.0	55.6	60.4	63.6	71.6	80.5	86.6	94.6	98.1	100
Lenzites saepiaria	21.5	33.4	43.0	70.0	82.1	91.2	96.0	100								
Polyporus leucospongia	11.2	20.7	39.0	72.0	83.3	90.0	96.0	100								
Polyporus ursinus	12.4	18.5	23.6	46.2	53.4	60.2	66.4	79.3	83.2	85.8	93.0	99.0	100			
Polyporus alboluteus	18.7	20.9	27.2	50.8	60.0	72.3	80.7	97.9	100							

The experiments, the results of which are shown in tables I and II, were conducted at Boulder, Colorado, during the winter and spring of 1928–29. The actual laboratory work with the eleven plants listed was carried on in as rapid a succession as physically possible, so that conditions of relative humidity, room temperature, and air movements would affect all eleven plants equally.

The fungus specimens used in the following experiments were collected during the summer previous to the experiments, air-dried, and then packed away in paper sacks. The number of specimens used in each of the experiments varied according to their size; of some species, as many as twenty fruiting bodies were employed, whereas of others, fewer or only one. The specimen, or specimens, for each of the eleven species was first weighed dry; then, one at a time, they were immersed in tap-water for a period of ten minutes, removed from the water and weighed again, immersed for another ten minutes, and so on until they had been immersed for one hour.

After the experiments on the absorption of water were completed, these same specimens were used to ascertain the rate of water loss by evaporation. They were weighed at intervals as shown in the table, and the percentage of loss in weight was calculated.

The data in these tables were obtained from five separate experiments conducted at different times and with different specimens. In repeating the work five times and using different specimens, very little variation was shown. In no case was the variation in excess of 2 per cent.

The rate of water absorption, the percentage of water held, as well as the rate of water loss by evaporation, is by no means the sole solution for the altitudinal distribution of macrofungi in the Rocky Mountains, but it seems that the water relations play an important role, especially in the case of respiration.[20] Distribution cannot be based upon any one single factor, for undoubtedly several factors are involved. The water used by a fungus for its physiological functions is obtained from the substratum by

[20] Richards, F. J. The relation between respiration and water content in higher fungi. New Phytol. **26:** 187–201. 1927.

absorption and conduction,[21] by the absorption of rain water which falls upon the surfaces of the sporophores, and from the moisture in the air. At high elevations, a sporophore which can absorb quickly a large quantity of water is unquestionably at a greater advantage than one in which the reverse conditions exist, for at this elevation showers are usually of short duration during the summer.

All of the pore fungi growing near timberline are wood-inhabiting. They may be found upon corticated and decorticated logs, very rarely upon living trees. If the logs still retain their bark, rain water can percolate through the cracks in the bark and keep the wood moderately moist. The bark, however, soon falls off, thus exposing the wood. The outer crust of this exposed wood becomes hard, cracked, and dry; the inner core dries out less rapidly and affords better moisture conditions for fungous growth. Thus, one frequently finds logs in which the center is entirely rotted out, whereas the outer crust is made up of apparently sound wood. If some logs have growing from them several sporophores of *Polyporus leucospongia* or *P. alboluteus*, which can absorb a large quantity of water based on their air-dry weights during a shower of one hour's duration, then these saturated sporophores can give water to their substrata in a manner similar to that in which a saturated sponge can give water to a piece of filter paper. These sporophores probably hold this great quantity of water intercellularly by capillary attraction, and by the forces set up by the colloidal nature of the outside of the walls of the hyphae. The supply of water taken into the cells by the force of suction pressure evidently does not enter into this problem in this respect, for it can scarcely be conceived that a substratum could take water from the living protoplasm of fungous hyphae which apparently have a relatively high suction pressure. Since the writer on several occasions has observed that after a rain of short duration the sporophores apparently do convey some water to the substratum, it is thought that the water is conveyed from the saturated sporophores to the substratum by the force of capillarity. Additional forces which may be involved are the outside atmos-

[21] Pieschel, E. Ueber die Transpiration und Wasservorsorgung der Hymenomyceten. Bot. Archiv 8: 64–104. 1924.

pheric pressure and the weight of the water column in the saturated sporophore.

The fungi growing at timberline are exposed to the drying effects of high winds, bright sun, and low relative humidity. They begin their growth in the spring and early summer, during which time they are watered from melting snow. Later in the summer, and when the snow has disappeared, the fungi receive their supply of water from daily showers of short duration; but during the remainder of the day they are exposed to conditions which bring about partial desiccation. It is obvious that the sporophores obtain some water from the substratum, but this supply gradually diminishes as the season advances, for it is evident that the logs, which are subjected to the same desiccating influences as the sporophores, would likewise dry out to some extent, and that the amount of water absorbed by them during the showers of short duration would not be sufficient to offset the loss by evaporation during the sunny hours of the day.

In all species that demonstrate the ability to absorb water quickly and in large quantities, as *Polyporus alboluteus* and *P. leucospongia*, the cell walls of the context are always very thick; also, the surface of the sporophore is roughly clothed or else spongy and absorbent.

From the graph (fig. 1) it can be seen that *Polyporus alboluteus* and *P. leucospongia* are outstanding in their ability to absorb a large quantity of water quickly. Furthermore, the graph shows that these two species have an additional advantage in the slowness with which they dry out, especially as they approach complete desiccation. These two species, as has been noted previously, are found chiefly in the montane and subalpine zones between 9,500 and 11,500 feet elevation.

In the case of *Lenzites saepiaria*, which is distributed from the foothill region to timberline between 6,000 and 11,500 feet elevation, the graph shows that while this fungus absorbs water less rapidly than the two preceding species, it nevertheless approaches its maximum water-holding capacity more quickly and is able to retain the water to the same extent as the species mentioned above. Thus the three species of fungi found at timberline absorb water at different rates, but appear to have in common the

ability to hold water somewhat tenaciously as they approach desiccation.

So far, the three species that grow at a high elevation have been discussed. By way of contrast, the graphs of these three species should be compared with those of *Polyporus versicolor*, *P. adustus*, and *Trametes hispida*, which are found only in the lower elevations

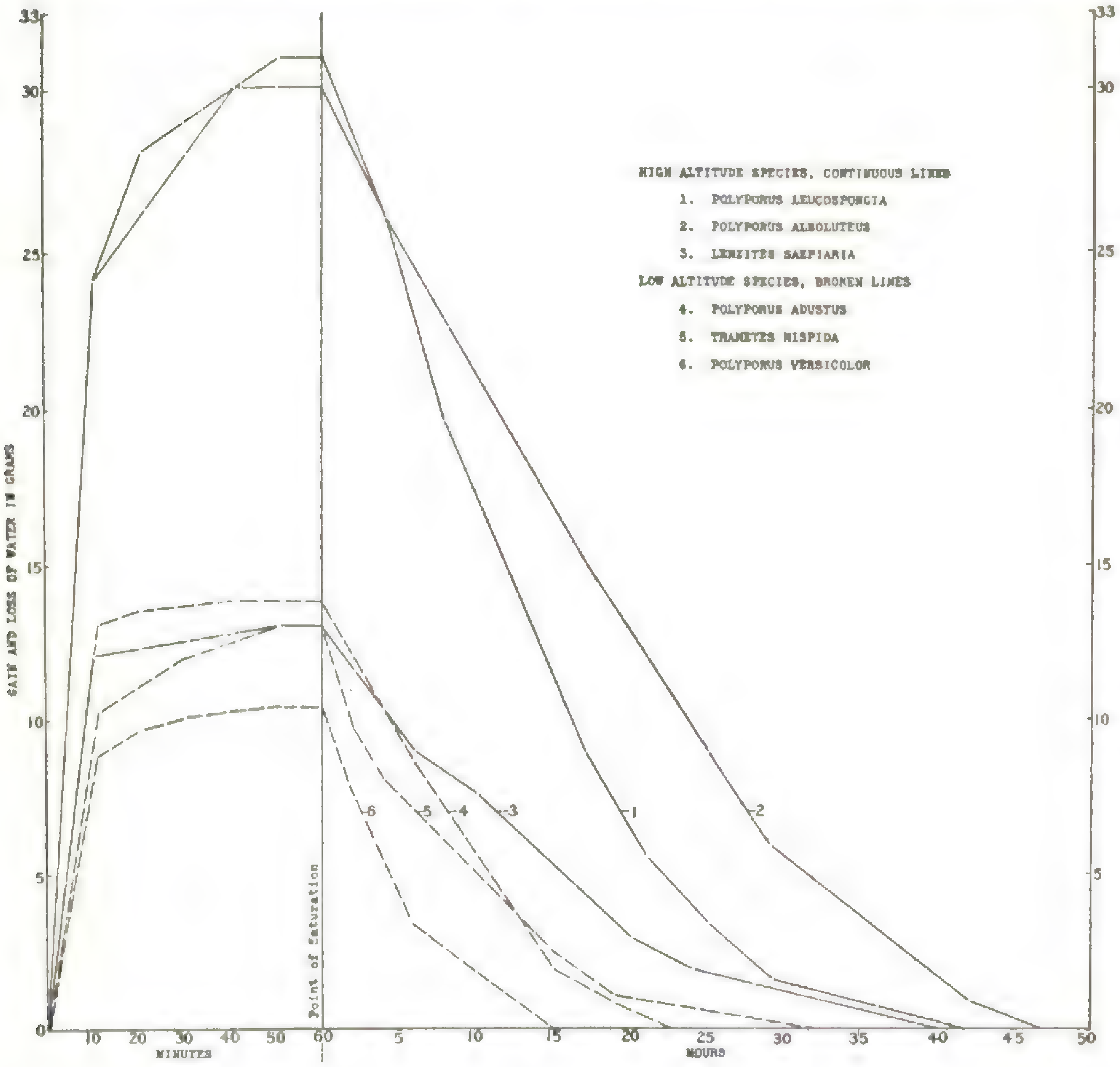


Fig. 1. Graph based on 5 grams air-dry weight of fungous material.

and never extend up to timberline, that is between elevations of 5,000 and 8,000 feet. They are of common occurrence in the plains where they grow on cottonwoods (*Populus* spp.) and willows (*Salix* spp.). In Colorado, they make their growth mainly in the spring when the logs and stumps to which they are attached are still moist from the winter's melting snow and from the spring

rains. They begin their growth surprisingly early in the season; in fact the writer has observed growth to take place as early as February and the sporophores to be fully developed by the early part of May. Furthermore, growth in midsummer takes place only during exceptionally wet summers. In the plains and foothill zones, daily showers are rare during the summer, whereas near timberline they are of common occurrence and to be expected.

On examination of the graph of these three low-altitude species, it is seen that they absorb water at approximately the same rate and to the same extent, and reach their point of saturation almost as quickly, as does *Lenzites saepiaria*. On the other hand, they appear to dry out more quickly and their retention of water as the point of complete desiccation is approached does not appear to be as pronounced as in the high-altitude species. Yet, in proportion to the amount of water absorbed, the low-altitude species appear to retain their moisture more tenaciously.

After the discussion of the water relations of pore fungi found at the two altitudinal extremes, additional light may be thrown on the problem by discussing various species found between these two altitudinal extremes.

In the *Fomes*-forms, especially *Fomes Pini* and *F. pinicola*, factors other than those mentioned for *Polyporus alboluteus* and *P. leucospongia* are involved. These two *Fomes*, which are found throughout the mountainous regions wherever suitable host-plants occur, can absorb a maximum of only 150 to 190 per cent water based on their air-dry weights. Because of their dense structure and their great size, desiccation of their sporophores takes place slowly. In dry regions, such as the foothill zone and the upper limits of the subalpine zone, these species are found to grow close to the ground. In such a position, they have the advantage of shade, high relative humidity, and in some cases, water absorption directly from the forest litter. In the more moist and more humid Engelmann spruce (*Picea Engelmanni*) belt, these species may be found growing from eight to ten feet above the ground.

Fomes Pini and *F. pinicola* are somewhat widespread in distribution, and observations show that the former species extends slightly farther into the dry regions than the latter. The sporo-

phore of *Fomes pinicola,* when growing on conifers, becomes covered with a resin-like secretion which renders the upper surface of the fructification more or less impervious to water and checks evaporation (pl. 33). No such condition exists in *Fomes Pini.* The hymenia of these species show a rate of water absorption opposite to that shown for the sporophores. To illustrate this, one square inch of the hymenium was cut out from large sporophores of the two species and all but the pore-mouths was covered with warm paraffin. After one minute's immersion in water, *Fomes pinicola* absorbed 2.5 grams of water, whereas the other species absorbed only 1.4 grams, or a little more than one-half the quantity of the former species. Prolonged soaking showed this difference to persist, but the difference became less marked. The water absorbed on prolonged soaking, however, is of less consequence than that absorbed during the first minute. The fact that the hymenium of *Fomes pinicola* absorbed water very much faster than the hymenium of *Fomes Pini* would indicate that the former species could likewise absorb more moisture from the atmosphere than the latter. The importance of the hymenium in gathering water from a humid atmosphere should not be overlooked, for it is in this part of the sporophore that growth takes place. In the case of *Fomes pinicola,* even though it has a resinous coating which checks evaporation and a hymenium which absorbs more moisture from the air, the fact that very little water can be absorbed by the resinous surface of the fruiting body from the rains appears to place this fungus at a slight disadvantage when compared with *Fomes Pini.*

Polyporus ursinus is an interesting fungus with reference to water absorption and water loss. It is comparatively heavy for its unit volume even when air-dried. This species does not take up such a large quantity of water, but, like *Polyporus leucospongia,* its swelling is very pronounced (pl. 19, figs. 5–8). *Polyporus ursinus, Trametes odorata,* and *T. subrosea* for some reason are limited to the moist regions of the mountains. Their rates of water absorption and evaporation show relatively little of significance that might pertain to their distribution.

In conclusion to the discussion on the distribution of pore fungi in Colorado, it appears that spore germination is probably not

a limiting factor. Some data are presented for the first time which at least indicate that the water relations of species of pore fungi may be one of the important factors in restricting their altitudinal distribution. It is brought out in the preceding discussion that, at least in the Rocky Mountains, the distribution of any one species of pore fungus is not in all cases coextensive with that of its host-plant.

III. The Family Polyporaceae

MATERIALS AND METHODS

In the microscopical examination of materials, the free-hand sectioning method has been used. The procedure is briefly as follows: A small piece of the dried material to be sectioned is placed in 95 per cent alcohol for one or two minutes in order to drive out the air; it is then transferred to water and allowed to soak for several minutes, or until soft, and then cut in elder pith according to the usual procedure followed by Burt and Overholts. While cutting the sections, the razor blade is kept flooded with 95 per cent alcohol in order to prevent curling of the sections, and the cut sections are then transferred to a slide upon which was previously placed a drop of 10 per cent KOH solution. After a sufficient number of sections are thus cut and transferred to the drop of KOH on the slide, a drop of 3–5 per cent water-soluble eosin is added to the KOH; a cover glass is placed over the material, and the slide is ready to be examined under the microscope. All measurements and drawings were made from sections mounted in this eosin-KOH solution, for it was felt that the KOH swells the material to approximately natural size. In species having a dark-colored context, KOH rendered sections rather dark in color, and in mounting sections from such plants the lactophenol-cotton blue[22] mounting medium has been found to be satisfactory. This mounting medium likewise causes the material to swell to approximately that of fresh material, and in general it seems to be a superior stain for mycological work. Permanent mounts are made by using this medium.

In making observations on the hyphae of the context, the same

[22] Linder, D. H. An ideal mounting medium for mycologists. Science, N. S. **70**: 430. 1929.

procedure as stated above is followed; but instead of sectioning the material, it is preferable to tease it out with needles, for this method gives a better mount for the study of hyphal characters. In fructifications with a colored context, staining is unnecessary, for the hyphae will be sufficiently colored to afford good visibility.

The material examined in the preparation of this paper covers all of the collections known from Colorado and listed elsewhere.[23] The writer's herbarium, however, which includes collections of Colorado fungi over a period of eight years, represents the nucleus of materials used in the preparation of this treatise.

ACKNOWLEDGEMENTS

The writer wishes to express his sincere appreciation to the following individuals for the privilege of studying specimens in various herbaria: Dr. George T. Moore, Director of the Missouri Botanical Garden; Dr. Fred J. Seaver, Curator of the Mycological Herbarium in the New York Botanical Garden; Mr. John A. Stevenson, Senior Mycologist in Charge of the Mycological Collections, and Dr. George G. Hedgcock, Pathologist in the United States Department of Agriculture; Dr. L. O. Overholts, Professor of Botany in the Pennsylvania State College; Dr. L. W. Durrell, Professor of Botany in the Colorado Agricultural College; and Dr. Bessie B. Kanouse, Assistant to the Director and Curator in the University of Michigan.

For the use of photographs, the writer wishes to express his appreciation to Dr. L. O. Overholts and to Mr. John A. Stevenson.

Most sincere appreciation is expressed to the Board of Regents and the President of the University of Colorado, for granting a leave of absence on two different occasions from the above institution, in order that the writer could continue graduate study at the Missouri Botanical Garden; to the Trustees and the Director of the Missouri Botanical Garden, for fellowship grants and for the use of the facilities of the Garden. Lastly, the writer wishes to express his appreciation to Dr. L. O. Overholts, whose influence resulted in the beginning of this work eight years ago; to Dr. D. H. Linder, under whom the work was finally molded and com-

[23] Shope, P. F. History of mycological collectors in Colorado. Mycologia **21**: 292–296. 1929.

pleted, and to many others who offered kind assistance, advice, and encouragement in various ways.

MORPHOLOGY AND REPRODUCTION

The family Polyporaceae belongs to the Basidiomycetes, and is characterized by having tubes or cup-like depressions which are lined internally by the hymenium. Basidiospores are the chief organs of reproduction.

Basidia are produced from the terminal cells of hyphae which extend from the trama out into the hymenium. These terminal cells become club-shaped, or remain cylindric, and are usually of a greater diameter than the cells of the hyphae immediately back of them. In most cases, the living cells and the young basidia contain two nuclei. In the basidia, these two nuclei fuse, but later and at intervals that vary with the species there usually follow two divisions (meiosis) as a result of which the basidia, as a rule, have four nuclei. By this time four sterigmata (rarely fewer) have developed on each basidium, and at the apex of each sterigma is developed a small globose swelling. A single nucleus now passes up through each of the four sterigmata into the globose swellings at their apexes.[24] These swellings are later cut off at their bases by septa and develop into spores characteristic of the species. When the spores are mature they are ready to be discharged. At this stage, according to Buller,[25] a small drop of water is formed immediately below each spore. This droplet increases in size to approximately half the diameter of the spore, and then the spore, with the droplet attached, is suddenly shot off the sterigma for a distance of from 0.1 to 0.2 mm., following which the sterigma collapses.

On the advent of suitable environmental conditions, the basidiospores swell and later send out germ-tubes which become septate and every cell usually contains one nucleus. Sooner or later, some of these primary mycelial cells conjugate with other cells and become binucleate. The two nuclei resulting from this fusion do not immediately fuse, but lie side by side and divide simultaneously during subsequent growth of the hypha. The hyphae which develop from these binucleated cells have clamp connections and

[24] Vokes, M. M. Nuclear division and development of sterigmata in *Coprinus atramentarius*. Bot. Gaz. **41**: 194–205. 1931.

[25] Buller, A. H. R. Researches on fungi. **2**: 148–152. 1922.

are known as the "secondary mycelia." Sporophores are produced after a period of extensive growth of the secondary mycelium in the substratum, during which time reserve materials are probably collected and stored. In the sporophore, some of the secondary mycelium is utilized in the formation of various tissues, in which case the cells lose their individuality and become changed in shape and structure. These tissue-like mycelia are called "tertiary mycelia."

The stimulus of gravity plays an important role in controlling the direction of growth of the fruiting bodies of fungi (see Atkinson's 'Mushrooms,' p. 15, and Buller's 'Researches,' **2**: 110.). The pore layer is positively geotropic, whereas the hymenium lining this layer is transversely geotropic. If a tree bearing sporophores is felled, subsequent growth of these sporophores will be controlled by the new stimulus established by the change in horizontal-vertical position. The positive geotropic response of the tubes appears to be an aid in the discharge and dispersal of spores. In some species of *Fomes*, fruiting layers other than the last formed one may also discharge spores.[26]

Spores other than basidiospores (asexual spores, conidia, or chlamydospores) are variously produced in the vegetative or reproductive stages when environmental conditions are suitable.[27] These spores germinate and probably give rise to new plants.

Heterothallism and homothallism, which have been definitely proved for many species of gill fungi, have received little attention in the pore fungi. Heterothallism has been shown by Mounce[28] to occur in several species of the Polyporaceae.

CLASSIFICATION

The family limitations of the Polyporaceae followed in this paper are those of Gaümann and Dodge.[29] Killermann,[30] in a

[26] Buller, A. H. R. Researches on fungi. **2**: 108. 1922.

[27] Snell, W. H. Chlamydospores of *Fomes officinalis* in nature. Phytopath. **11**: 173–174. 1921.

[28] Mounce, Irene. Notes on sexuality in *Fomes pinicola, F. roseus, Polyporus Tuckahoe, P. resinosus, P. anceps, Lenzites saepiaria, Trametes protracta,* and *T. suaveolens*. Can. Phytopath. Soc. Proc. **1929**: 27–28. 1930.

[29] Gaümann, E. A. & C. W. Dodge, Comparative morphology of the fungi. p. 430. New York, 1928.

[30] Killermann, S. in Engler, A. & K. Prantl, Die Natürlichen Pflanzenfamilien. **6**: 169. Leipzig, 1928.

recent issue of 'Die Natürlichen Pflanzenfamilien,' following the classification previously used in that series of publications, includes in the family the tribes Merulieae, Fistulineae, and Boleteae, as well as Polyporeae.

Genera of the Polyporaceae found in Colorado are: *Polyporus* (including *Polystictus*), *Fomes*, *Lenzites*, *Trametes*, *Favolus*, *Ganoderma*, and *Poria*. *Polyporus* and *Favolus* are always annual plants, whereas all the others listed may be annual or perennial. *Lenzites*, when perennial, does not have stratified lamellae-layers, whereas in all the other perennial genera the annual increments of growth are stratified. *Poria* is always resupinate. *Ganoderma* has a varnished or dull, thick crust, and the spores are always truncate and have a colored spiny endospore and a hyaline smooth exospore which collapses and gives the spore a spiny or warty appearance. *Fomes* is always perennial, but one-year-old sporophores may be confused with strictly annual genera. *Trametes* may be annual or perennial, but usually the sporophores are not as large as those of *Fomes*, and generally not ungulate. The genus *Trametes*, in most cases, differs from all other genera in the family by the fact that the tubes are joined to the context in an uneven line, so that they appear to be sunken into the context to unequal depths. This genus is a poorly marked one and it would probably be much better to disregard it entirely. Nevertheless, it is still used and recognized, and hence will be used in this paper. No trouble, however, should be experienced in the use of the key, for all species of the genus *Trametes* are included in the key to the species of *Polyporus*. Of the annual forms, *Polyporus* most frequently has circular or angular pore-mouths, whereas *Favolus* has large radially arranged and radially elongated ones. Following the procedure of Overholts[31] and Rhoads,[32] the genus *Polystictus* is not recognized on account of its indefinite and transitional character. A historical account of this family and its genera may be found elsewhere.[33]

[31] Overholts, L. O. Polyporaceae of the middle-western United States. Wash. Univ. Studies 3: 3–96. 1915.

[32] Rhoads, A. S. The biology of *Polyporus pargamenus* Fr. N. Y. State Coll. For. Tech. Publ. No. 11. **18**: 15. 1918.

[33] Overholts, L. O. Comparative studies in the Polyporaceae. Ann. Mo. Bot. Gard. **2**: 667–671. 1915.

Following American usage, the old established generic names are used throughout this paper. Of the various segregates that have been proposed, the genus *Ganoderma* appears to be well marked. Its macro- and microscopical characters are sufficiently distinct to warrant its segregation. This genus is the only one of the many segregates that has met with at least partial acceptance in America.[34]

Additional genera, as *Cyclomyces, Daedalea,* and others, are found in the family Polyporaceae, but since they have not as yet been reported from Colorado a consideration of them is unnecessary here.

Up to comparatively recent times, the classification of the Polyporaceae was based only on external appearances. This system became unsatisfactory partly because of the great increase in the number of species, and also because of the change in the gross morphology induced by different environments. Recently, the microscopical structures of the fructifications have been taken into consideration, along with the macroscopical ones, thus defining species more clearly and definitely. Microscopical structures have been used by Burt[35] in his work with the Thelephoraceae; by Kauffman[36, 37] with the Agaricaceae and Clavariaceae; and by Bourdot and Galzin[38] with the Hymenomycetes in general. Overholts[39] has brought together and described the various microscopical characters used in the taxonomy of the Hymenomycetes. For convenience, a brief description of the microscopical characters used in this paper will follow.

In the Polyporaceae, hyphae vary in thickness from 1.5 to 15 microns. In a particular species, variations in hyphal thickness usually fall within comparatively narrow confines, the tramal hyphae being somewhat thinner than those of the context. Also,

[34] Haddow, W. R. Studies in Ganoderma. Jour. Arnold Arbor. **12**: 25–46. 1931.

[35] Burt, E. A. Thelephoraceae of North America. Ann. Mo. Bot. Gard. **1–13.** 1914–26.

[36] Kauffman, C. H. The Agaricaceae of Michigan. Mich. Geol. and Biol. Survey, Publ. 26. Biol. Ser. 5. 1918.

[37] ————, Cystidia in the genus Clavaria and some undescribed species. Mich. Acad. Sci., Arts and Letters, Papers **8**: 141–151. 1927.

[38] Bourdot, H. & A. Galzin, Hyménomycètes de France. Paris, 1927.

[39] Overholts, L. O. Research methods in the taxonomy of the Hymenomycetes. Proc. Internat. Cong. Pl. Sci. **2**: 1688–1712. 1929.

thick-walled "vascular" hyphae, with apparently no cross-walls, may be of slightly greater diameter than ordinary vegetative hyphae. Septations are often difficult to see and apparently absent in some hyphae. Thickness of cell-walls is also variable; it is not uncommon to find cell-walls of greater thickness than the diameter of the lumen. The walls may be nodose or smooth.

Hyphae within a given field of the microscope are found to be branched or simple; occasionally, they are dichotomously or otherwise branched and in some few cases, hyphal complexes are found. In these complexes, the hyphal branches are numerous and of smaller diameter than the parent hypha from which they spring. Hyphal fusions are sometimes observed, in which case the hyphae fuse in a manner similar to the letter H.

Clamp connections may be abundant or apparently absent depending upon the species. Where the hyphae are of extremely small diameter, these clamp connections are visible only under the oil immersion lens. They may appear over every septum in a hypha, or else widely scattered.

Incrusted hyphae are not extremely frequent in the Polyporaceae. When present, they have small, colorless, crystalline bodies attached to the outside of their wall and which are sometimes completely soluble in KOH solution. Incrusted cystidia (pl. 19, fig. 8) are often encountered. Occasionally, crystalline bodies having a diameter several times that of the hyphae may be found in the trama (*Lenzites serpens* Fr.).

Setae and cystidia are prominent sterile organs found in the hymenium or trama. They usually extend beyond the general limit of the hymenium, and differ from each other only in color, especially after KOH solution has been added. When mounted in KOH solution, cystidia appear hyaline, yellowish, or light brown under the microscope; whereas setae appear very dark brown to black. In the following line drawings of these organs, cystidia are outlined, whereas setae are shaded. Both setae and cystidia may or may not be incrusted. Setae are found only in species having dark-colored contexts, whereas cystidia are found in species having either light- or dark-colored contexts.

Hyphal pegs are compound hyphal fasciculate projections extending beyond the general level of the hymenium (pl. 17, fig. 2).

These pegs are made up of two or more hyphae arranged parallel to each other, or else interwoven. The hyphae may or may not be incrusted or gelatinized.

Paraphyses in the Polyporaceae are usually either club-shaped or cylindric and show little difference in form or structure in different genera and species. They are seldom found to have characteristic markings or shapes as are found in many species of *Aleurodiscus* of the Thelephoraceae. Taxonomically, they are of little value in this family.

When sections of *Polyporus alboluteus, P. fibrillosus,* and probably some other species, are mounted in KOH solution, the tramal tissue turns a deep red. With these and some other species this reaction is of taxonomic value; also, the same color-change occasionally takes place in *Fomes pinicola,* but in this case it is not a dependable taxonomic character.

As has been stated previously, KOH solution turns the hyphae of species with a brown context to a markedly darker color. While this is not of great taxonomic importance here, in related families within the order the reaction of KOH solution on the hyphae has proved of value.

The presence of a black line in the context of several species of pore fungi appears to be a constant factor of taxonomic importance. Such a black line is found in *Fomes nigrolimitatus, F. conchatus, Trametes stereoides, Polyporus ovinus,* and *P. osseus.*

In general, an attempt has been made to follow the International Rules for Nomenclature.

Ridgway's[40] 'Color Standard and Color Nomenclature' has been used in the following scientific descriptions, in which case the first letter of the color-name is always capitalized.

Keys and Descriptions

KEY TO THE GENERA

Sporophores entirely resupinate and remaining so throughout the growing period . . . . *Poria* (p. 395)

Sporophores not resupinate; stipitate, sessile, or effused-reflexed. 1

1. Spores minutely spined; surface of the pileus covered with a shiny or dull thick crust. . . . . *Ganoderma* (p. 373)

Spores smooth; surface of the pileus anoderm or covered with a thin crust. 2

[40] Ridgway, R. Color standard and color nomenclature. Washington, D. C. 1912.

2. Pore-mouths angular, large, and radially elongated; stipe short, lateral, or excentric. . . . . *Favolus* (p. 394)
   Pore-mouths circular or angular, usually small, not radially elongated; stipe present and central or excentric, or entirely absent. 3
3. Plants perennial; poroid; producing a new layer of tubes each year. 4
   Plants perennial; lamellate. . . . . *Lenzites* (p. 390)
   Plants annual; producing only one layer of pores. 5
4. Sporophores large and massive; ungulate. . . . . *Fomes* (p. 376)
   Sporophores smaller than above; not usually ungulate. . . . . *Trametes* (p. 362)
5. Fruiting layer definitely poroid. 6
   Fruiting layer more or less lamellate. . . . . *Lenzites* (p. 390)
6. Tubes joined to the context along a straight line. . . . . *Polyporus* (p. 317)
   Tubes joined to the context along an uneven line, *i.e.* tubes are sunken to unequal depths in the context. . . . . *Trametes* (p. 362)

POLYPORUS

Polyporus (Mich.) Fries, Syst. Myc. **1**: 341. 1821; Mich. Nov. Plant. Gen. p. 129. 1729.

Plants annual, terrestrial, or lignicolous, sessile, effused-reflexed, or stipitate, fleshy, coriaceous, or woody; context of various thicknesses and colors, homogeneous or duplex, zonate or azonate; context and tramal tissue different in structure; tubes joining the context in a straight line; pore-mouths circular to irregular, rarely daedaloid or favoloid; edge of the dissepiments even, dentate, or toothed; spores variously shaped and colored; cystidia, setae, and hyphal pegs present or absent.

As defined in this paper, the genera *Polyporus* and *Favolus* contain only annual plants, whereas all other genera of the family considered in this treatise are either annual or perennial except *Fomes*, which is always at length perennial.

It is very difficult to draw definite lines of distinction between the genera *Polyporus* and *Trametes*, and in all probability no well-marked ones exist. It seems advisable, however, to retain the genus *Trametes*, due to the fact that it still meets with favor. Hence, in order to avoid confusion, all species of the genus *Trametes* are keyed out in the key to the species of *Polyporus* as well as in the key to the species of *Trametes*.

The various synonyms of this genus may be obtained from the lists of synonyms accompanying the following species.

KEY TO THE SPECIES[41]

Sporophores sessile or effused-reflexed; never stipitate..........Section 1 (p. 318)
Sporophores centrally, excentrically, or laterally stipitate.........Section 2 (p. 320)

Section 1

Context white, whitish, very light yellow or light wood-color........Subdivision I
Context yellowish-red or reddish..............................Subdivision II
Context brown, darker than wood-color.........................Subdivision III

Subdivision I

Sporophores globose or door-knob shaped; hymenium internal and enclosed by a volva..*1. P. volvatus*
Sporophores not as above..1

1. Surface of the pileus in dried plants dark brown, dark reddish-brown, or blackish-brown; context white, very light brown or yellowish-brown........2
   Surface of the pileus white, whitish, gray, yellowish, or light brown..........8
2. Context more than 1 mm. thick; pileus usually more than 1 cm. thick........3
   Context less than 1 mm. thick; pileus always less than 1 cm. thick...........5
3. Surface azonate; cystidia present and incrusted; plants sodden when fresh. ....*9. P. ursinus*
   Surface with age becoming zonate; cystidia absent; plants sodden or not sodden when fresh..4
4. Surface fibrillose; plants sodden when fresh; pores 3–4 per mm.; plants small, usually less than 7 cm. in diameter.................*18. P. fragilis*
   Surface velvety-tomentose; not sodden when fresh; plants larger than the above..*15. P. resinosus*
5. Tubes less than 2 mm. long; pileus zonate, and multicolored................6
   Tubes more than 2 mm. long; pileus azonate or zonate, but not multicolored..7
6. Zones brown, reddish-brown, black, purple, greenish, or yellowish, some zones glabrous or nearly so................................*2. P. versicolor*
   Zones alternately villous-cinereous and orange-glabrous or nearly so ....*4. P. zonatus*
   Zones alternately brown and black..........................*21. P. planellus*
7. Mouths of tubes averaging 3 or more per mm............*37. Trametes serialis*
   Mouths of tubes averaging 1–2 per mm..............*38. Trametes variiformis*
8. Hymenium more or less smoke-colored or black..............................9
   Hymenium not as above...11
9. Hymenium eventually turning to a dark smoke-color, or nearly black........10
   Hymenium very light gray or smoke-colored...................*3. P. hirsutus*
10. Margin of the pileus crisped and wavy; pileus strigose towards the base, adpressedly fibrillose on the margin; sporophores always densely imbricated...*17. P. crispus*
    Margin of the pileus even, finely tomentose; sporophores usually not densely imbricated.......................................*16. P. adustus*
11. Pileus markedly zonate with alternate hirsute and pubescent zones..........12
    Pileus azonate, or if zonate, not with alternate hirsute and pubescent zones..13

[41] A key based on the microscopical characters of the hymenium will be found interspersed with the descriptions of the species. This key represents the probable natural affinities within the section.

12. Pileus made up of many multicolored zones; margin of pileus usually white or yellowish and lighter than the rest. . . . . *2. P. versicolor*
Margin of the pileus concolorous; zones alternate villous-cinereous and orange-glabrous . . . . *4. P. zonatus*
13. Surface of the pileus soft and spongy; more or less watery and sodden when fresh. 14
Surface of the pileus not as above; not sodden when fresh. 17
14. Tubes markedly collapsed when dry; plants fragrant when fresh. . . *22. P. spumeus*
Tubes only slightly or not at all collapsed when dry; plants not fragrant when fresh. 15
15. Cystidia present, extending only slightly beyond the basidia. . . . . . *12. P. borealis*
Cystidia absent 16
16. Tubes turning blue when touched or bruised, drying caesius; context not duplex. . . . . *14. P. caesius*
Tubes not turning blue when touched or bruised; context duplex, cottony above, horny below . . . . *5. P. leucospongia*
17. Mouths very large, 1 mm. or more in diameter, white or yellowish; dissepiments often lacerate. . . . . *39. Trametes heteromorpha*
Mouths less than 1 mm. in diameter; dissepiments lacerate or not lacerate. . . 18
18. Dissepiments with age lacerate; hymenium when young purplish, becoming yellowish with age 19
Dissepiments with age not becoming lacerate; hymenium never purplish in color 21
19. Pileus less than 4 mm. thick 20
Pileus more than 4 mm. thick. . . . . *8. P. subchartaceus*
20. Pileus usually conchate and attached to the substratum by a stalk-like attenuation; usually found growing on deciduous hosts. . . . . *7. P. pargamenus*
Pileus dimidiate and never with a stalk-like base; usually found growing on conifers. . . . . *6. P. abietinus*
21. Pileus when fresh becoming brown-spotted when touched . . . . *18. P. fragilis*
Pileus when fresh not becoming brown-spotted when touched. 22
22. Pileus hirsute, white, yellowish-brown, or gray; azonate or indistinctly zonate; usually sessile . . . . *3. P. hirsutus*
Pileus adpressedly-tomentose, yellow or brown, effused-reflexed with a narrow reflexed portion. . . . . *37. Trametes serialis*
Pileus minutely downy, white to cream-colored . . . . *20. P. anceps*

Subdivision II

Plants soft and spongy when fresh, drying brittle; on dead wood of conifers; turn red when KOH solution is added. 1
Plants tough or rigid when fresh, drying coriaceous to rigid; found on both coniferous and deciduous hosts; do not turn red when KOH is added. 2
1. Pores large, 1–3 mm. broad, dissepiments soon becoming lacerate; tubes 1–3 cm. long; plants mostly resupinate with occasionally a narrow reflexed margin. . . . . *10. P. alboluteus*
Pores smaller than the above, 1–2 per mm., dissepiments becoming lacerate; tubes 2–6 mm. long; plants sessile. . . . . *11. P. fibrillosus*
2. Pileus orange to cinnabar-red, fading with age; tubes 1–5 mm. long; mouths cinnabar-red; on deciduous wood. . . . . *19. P. cinnabarinus*
Pileus rose-colored to brownish; tubes indistinctly stratified in old plants; mouths rose-colored; mainly on conifers. . . . . *43. Trametes subrosea*

Subdivision III

Context light brown (if very light yellowish-brown, see Sub. I.)............1
Context darker; cinnamon-brown to rusty-brown..........................7
1. Pileus covered with a dense brown strigose pubescence....*41. Trametes hispida*
Pileus not clothed as above, velvety-tomentose to glabrous................2
2. Context less than 1 mm. thick..4
Context more than 1 mm. thick..3
3. Mouths averaging 4–6 per mm., circular.....................*15. P. resinosus*
Mouths averaging 1–2 per mm., usually daedaloid to labyrinthiform. ....*56. Lenzites trabea*
4. Dissepiments becoming lacerate with age; hymenium purplish in young specimens..5
Dissepiments not becoming lacerate; hymenium brownish...................6
5. Pileus usually conchate and attached to the substratum by a stalk-like attenuation; usually found growing on deciduous hosts.....*7. P. pargamenus*
Pileus dimidiate and never with a stalk-like base; usually found growing on conifers...*6. P. abietinus*
6. Mouths averaging 5–6 per mm............................*21. P. planellus*
Mouths averaging 1 per mm.......................*40. Trametes stereoides*
7. Setae present; cystidia absent; on coniferous wood only....................8
Cystidia present; setae absent; growing on coniferous wood or on the ground near coniferous trees; usually stipitate, but not always... ....*24. P. Schweinitzii*
Neither setae nor cystidia present in the hymenium.....................11
8. Context containing a thin black line which is less than 1 mm. thick..........9
Context not containing a black line as above..........................10
9. Fungus confined to coniferous hosts.................*47. Fomes nigrolimitatus*
Fungus confined to deciduous hosts....................*50. Fomes conchatus*
10. Spores globose to subglobose; margin yellowish, pileus dark brown ....*46. Fomes Pini*
Spores cylindric; margin concolorous with the surface of the pileus. ....*36. Trametes isabellina*
11. Context containing a central granular core....................*13. P. Rheades*
Context homogeneous..12
12. Dissepiments thin, less than 200 μ.......................*56. Lenzites trabea*
Dissepiments very thick, more than 200 μ................*42. Trametes odorata*

Section 2. Stipitate

Context white, whitish, very light yellow, or light brown............Subdivision I
Context dark-brown...Subdivision II
Context pinkish or reddish in color.............................*27. P. confluens*

Subdivision I

Stem black at the base...1
Stem not black at the base...3
1. Pileus large, 10 cm. or more in diameter; pileus covered with appressed scales; pores very large and angular, 1–4 mm. broad..........*31. P. squamosus*
Pileus smaller than the above; no scales present...........................2
2. Pileus glabrous or pruinose; concolorous throughout..............*34. P. elegans*
Pileus radially fibrillose; at times multicolored with reddish-brown or blackish splotches, especially near the margin..................*33. P. varius*

3. Context duplex, cottony above, horny below in dried plants; pileus and stem fawn-colored, hirsute; setae present.......................... *25. P. circinatus*
Context not duplex; no setae present.. 4
4. Context in fresh plants white to light rose-color, occasionally reddish next to the tubes, drying pinkish.......................... *27. P. confluens*
Context white in fresh plants and not turning pinkish on drying.............. 5
5. Stem central or excentric, never lateral..................................... 6
Stem lateral.. 7
6. Pileus white or grayish-white, less than 5 cm. in diameter and 3–4 mm. thick; stipe obese; pileus not becoming black-spotted on drying; plants usually attached to dead grass roots........................ *30. P. cryptopus*
Pileus white or tan, larger than the above, usually more than 5 cm. in diameter and 3–10 mm. thick; stipe obese; pileus becoming black-spotted on drying... *26. P. ovinus*
Pileus golden-brown to dark-brown; growing on deciduous wood.. *23. P. arcularius*
Pileus purplish to grayish-brown; growing on the ground and attached to buried wood.. *32. P. hirtus*
7. Plants growing on the ground and attached to buried wood; pileus 5–14 cm. in diameter; purplish to grayish-brown...................... *32. P. hirtus*
Plants wood-inhabiting; pileus less than 5 cm. in diameter; pilei imbricated. .... *35. P. osseus*

Subdivision II

Context less than 1 mm. thick; plants growing on the ground................ 1
Context more than 1 mm. thick; plants growing on wood or attached to buried wood... 2
1. Surface of the pileus shining and with a silky striation, reddish brown .... *29. P. cinnamomeus*
Surface of the pileus not shining, not silky, dull brown..... *28. P. perennis*
2. Context decidedly duplex; setae present...................... *25. P. circinatus*
Context not duplex; cystidia present; setae absent......... *24. P. Schweinitzii*

Section I. Sporophores sessile or effused-reflexed, never stipitate. I. Hemiangiocarpeae.

1. **Polyporus volvatus** Pk. Ann. Rept. N. Y. State Mus. **27:** 98. 1877.

Polyporus obvolutus Berk. & Cooke, Grevillea **7:** 1. 1878.
Polyporus inflatus Ellis & Mart. Am. Nat. **18:** 722. 1884.
Polyporus volvatus Helix P. Henn. Hedwigia **37:** 273. 1898.
Ungulina volvata (Pk.) Pat. Ess. Tax. Hymen. p. 102. 1900.
Cryptoporus volvatus (Pk.) Shear, Bull. Torr. Bot. Club **29:** 450. 1902.
Ungulina volvata var. *pleurostoma* (Pk.) Pat. Bull. Soc. Myc. Fr. **23:** 74. 1907.

Plate 16, fig. 1.

Pileus globose or compressed globose, sessile or very rarely stipitate, usually growing from insect bore-holes, 1–3 x 1–6 x 1–4 cm.; upper surface at first resinous, shining, becoming cracked, Light Ochraceous-Buff to Stanford's Brown; the resinous secretion may extend down over the volva, but it soon flakes off, revealing the soft, pubescent, white to Light Pinkish Cinnamon context; margin rounded and continuous with the volva, volva at first unbroken, later there develops 1 (rarely 2 or 3) circular or irregular (rarely elongated) openings, 3–6(10) mm. in diameter; context white, drying Light Buff to Warm Buff, 2–10 mm. thick, hyphae of the context grayish under the microscope, branched, undulating, 3–4 μ in diameter; tubes at first white, with age and on drying turning Light Ochraceous-Buff to Yellow Ocher, attenuated at the mouths into a very small opening, 2–10 mm. long; mouths very small, at first white, later Wood Brown, Snuff Brown to Brussels Brown, circular to angular, averaging about 3 per mm.; dissepiments grayish under the microscope, tapered, thickest at the mouths, mouth-end abruptly angled and often flat; hymenium 16–20 μ thick, loosely arranged, covering the bottom and sides of the tubes, occasionally also over the ends of the dissepiments; basidia 6–8 μ in diameter, hyaline; spores smooth, hyaline under the microscope, oblong-ellipsoid, apiculate, 10–13(15) x 4.5–6 μ.

Habitat: on various coniferous hosts.

Occurrence: uncommon. Spring.

Distribution: foothills and montane zones. Wide-spread throughout the coniferous regions of the United States.

Type of rot: white rot.

Polyporus volvatus is hemiangiocarpous in its development and thus forms a natural connecting-link with the Boletaceae of the Agaricales. The occasional presence of the hymenium on the free ends of the dissepiments indicates a conection with *Merulius.*

This fungus has been collected several times upon recently wind-felled rock pines (*Pinus scopulorum*) upon which the green needles still persisted. Such collections would indicate at least a partial parasitic relation between the fungus and the host which has previously been noted by Schmitz.[42]

[42] Schmitz, H. Jour. Gen. Physiol. 3: 795–796. 1921.

Insects probably play an important role in the distribution of the spores. They enter the volva through the opening, evidently to feed upon the discharged spores which have collected on the inside of the volva and thus their bodies become dusted over with the spores as they crawl around in the inside of the volva.

Zeller[43] has noted hyaline, pyriform, or oval conidia in this species.

II. Gymnocarpeae.

1. Hyphal pegs present; no cystidia or setae; spores 5–8 μ long.

2. **Polyporus versicolor** (L.) Fries, Syst. Myc. **1**: 369. 1821.
Boletus versicolor L. Sp. Pl. p. 1176. 1753.
Polyporus hirsutulus Schw. Trans. Am. Phil. Soc. II. **4**: 156. 1832.
Polystictus azureus Fries, Nov. Symb. p. 93. 1851.
Coriolus versicolor (L.) Quél. Ench. Fung. p. 175. 1886.
Polystictus versicolor (L.) Sacc. Syll. Fung. **6**. 253. 1888.
Coriolus hirsutulus (Schw.) Murr. Bull. Torr. Bot. Club **32**: 643. 1906.

Plate 16, fig. 2.

Pilei coriaceous, imbricate, sessile or occasionally effused-reflexed, sometimes connate, dimidiate or conchate, frequently narrowed at the base and attached to the substratum by a stalk-like attenuation. 1–6 x 1–8 x 0.1–0.5 cm. (larger in the tropics); surface concentrically zonate, at first velvety tomentose, Pale Smoke Gray, Smoke Gray, Cinnamon-Buff or Clay Color; later and on expanding the tomentum is pulled away, revealing nearly glabrous, shining zones of various colors, as yellowish, brownish, reddish, and blackish; margin thin, entire or undulating, occasionally sterile below; context thin, 0.5–2 mm. thick (thicker in the tropics), white, hyphae of the context radially arranged, rarely branched, thick-walled, 5–11 μ in diameter; tubes 0.2–2(4) mm. long; mouths angular, irregular, white, Pallid Brownish Drab, Pinkish Buff to Tawny-Olive, averaging 3–5 per mm.; dissepiments entire, becoming slightly lacerate, 65–120 μ thick; hymenium 14–17 μ broad, compact; basidia 4–5 μ broad, projecting

[43] Zeller, S. M. Mycologia **7**: 121–125. 1915...

up to 5 μ; spores smooth, hyaline, oblong-allantoid, 5–8 x 1.5–2.5 μ; hyphal pegs present, hyaline, usually incrusted, and hyphae scarcely discernible, projecting up to 40 μ, 18–25 μ in diameter.

Habitat: deciduous wood; rarely on coniferous wood. Parasitic and saprophytic.

Distribution: plains and foothill zones. Widespread in the United States.

Occurrence: common. Spring and early summer.

Type of rot: white rot.

The surface of the pileus of *Polyporus versicolor* is made up of concentric and variously colored zones. It is, indeed, a beautiful plant when fully expanded and developed. A young and undeveloped plant does not show these variously colored zones, but is indistinctly zoned and tomentose over its entire surface. Such specimens are easily confused with *Polyporus hirsutus*, but collections having specimens of this nature will usually also have a few showing the variously colored zones. *Polyporus versicolor* differs from *P. zonatus* in that the zones of the latter species are orange or reddish-orange in color and never multi-colored as in the former species.

It is evident that *Polyporus versicolor, P. zonatus,* and *P. hirsutus* are all closely related, as is shown by the similarity of their microscopical structures. Hyphal pegs, spore size and shape, as well as other microscopical characters, are identical in all three plants. The differences in these three species lie primarily in the pubescence, zonation, and color of the surfaces of the pilei.

The biology of this species has been studied by Bayliss.[44]

3. **Polyporus hirsutus** (Wulf.) Fries, Syst. Myc. **1**: 367. 1821.

Boletus hirsutus Wulfen, in Jacq. Coll. **2**: 149. 1788. Not *Boletus hirsutus* Scop. 1772.

Boletus nigromarginatus Schw. Schr. Nat. Ges. Leipzig **1**: 98. 1822.

Polystictus hirtellus Fries, Nov. Symb. p. 83. 1851.

Polystictus hirsutus (Wulf.) Sacc. Syll. Fung. **6**: 257. 1888.

Coriolus nigromarginatus (Schw.) Murr. Bull. Torr. Bot. Club **32**: 649. 1906.

Plate 17, fig. 3.

[44] Bayliss, J. S. Jour. Econ. Biol. **2**: 1–22. 1908.

Pileus coriaceous to rigid, sessile or effused-reflexed, applanate, dimidiate or flabelliform, imbricate or solitary, 1–5 x 1–7 x 0.2–3 cm.; surface concentrically furrowed and zoned, erect-hirsute to fibrillose, occasionally with multicolored zones, but never with alternate multicolored glabrous and hirsute zones, color various, Yellow Ocher, Cinnamon-Rufus, Tawny to Grayish Olive or Pale Smoke Gray; margin either thin, entire or undulate, or thick and sharply rounded, finely tomentose, sterile below; context corky, sometimes zonate, white to Light Buff, 0.5–20 mm. thick (not including the tomentum), hyphae of the context hyaline, thick-walled, undulate, branched, 3–6 μ in diameter; tubes white, Light Buff or Pale Smoke Gray, 1–5 mm. long; mouths circular to angular, averaging 3–4 per mm., white, Warm Buff, Clay Color, Buckthorn Brown, Pale Neutral Gray, or some other shade of light smoke color; dissepiments 80–160 μ thick; hymenium 12–16 μ thick, closely compact; basidia 5–6 μ broad; spores smooth, hyaline, cylindric or allantoid, 6–8(10) x 2–3 μ; hyphal pegs occasionally present, hyaline, usually incrusted, hyphae scarcely discernible, projecting up to 50 μ, 12–18 μ in diameter.

Habitat: various deciduous hosts, especially cottonwoods (*Populus* spp.) and aspen (*Populus tremuloides*); known to occur on *Abies*.

Distribution: from the plains zone up to the subalpine zone. Widespread in the United States.

Occurrence: common. Spring.

Type of rot: white rot.

The above description of *Polyporus hirsutus* represents the species in its broadest sense, and undoubtedly several segregates could be made. The thin *Polystictus*-like form is commonly encountered at low elevations, whereas a thick form with a light smoke-colored hymenium is found on aspen (*Populus tremuloides*) and narrow-leaved cottonwood (*Populus angustifolia*) at high elevations. The multicolored form, which is of uncommon occurrence, may easily be confused with *Polyporus zonatus*. The latter species, however, has a pronounced orange color, whereas *P. hirsutus* is white, gray, or pale yellowish in color.

4. **Polyporus zonatus** Fries, Syst. Myc. **1:** 368. 1821.
Coriolus zonatus (Fr.) Quél. Ench. Fung. p. 175. 1886.

Polystictus zonatus (Fr.) Sacc. Syll. Fung. **6**: 260. 1888.
Coriolus Lloydii Murr. N. Am. Fl. **9**: 23. 1907.
Polyporus Lloydii (Murr.) Overh. Wash. Univ. Studies **3**: 32. 1915.

Plate 16, fig. 3.

Pilei coriaceous, sessile or effused-reflexed, rarely connate, dimidiate or conchate, often narrowed at the base and attached by a stalk-like attenuation, 1–4 x 1–7 x 0.2–0.5 cm.; surface usually concentrically zonate with zones alternately adpressedly tomentose (rarely erect-tomentose) and glabrous, tomentose zones Pale Smoke Gray to Mouse Gray, glabrous zones Ochraceous-Buff to Zinc Orange; margin thin, entire or undulating, often as dark as Hazel or Kaiser Brown; context white, 0.5–2 mm. thick, hyphae of the context hyaline under the microscope, sparingly branched, 5–8(10) μ in diameter; tubes 1–3 mm. long, concolorous with the mouths; mouths white, Ochraceous-Buff to Ochraceous Tawny, angular, averaging 3 per mm.; dissepiments becoming lacerate with age, 60–160 μ thick; hymenium 12–16 μ thick, compact; basidia 5–6 μ broad; spores smooth, hyaline, oblong-allantoid, 6–8 x 2–3 μ; hyphal pegs present, hyaline, usually incrusted, hyphae scarcely discernible, projecting up to 40 μ and 12–18 μ in diameter.

Habitat: deciduous hosts.

Distribution: plains and foothill zones. Southern United States.

Occurrence: uncommon.

Type of rot: white rot.

When mature, this fungus is characterized by its thin pileus and alternately tomentose cinereous and glabrous reddish-orange-zoned surface. In young specimens, however, these glabrous zones are not evident. This species differs from *Polyporus hirsutus* in having a pronounced orange-colored pileus and thus approaches *Polyporus pubescens*.

5. **Polyporus leucospongia** Cooke & Hark. Grevillea **11**: 106. 1883.

Spongiporus leucospongia (Cooke & Hark.) Murr. Bull. Torr. Bot. Club **32**: 474. 1905.

Plate 17, figs. 1–2.

Pileus soft, spongy, effused-reflexed, occasionally sessile, dimidiate, 0.5–3 x 1–15 x 0.5–2 cm., sometimes laterally connate for 30 cm. or more; surface velvety-tomentose, subpelliculose with age, pellicle flexuous, never horny, thrown into folds or even, azonate, white, Light Buff, Pinkish Buff to Clay Color; margin rounded and inflexed, sterile, concolorous; context duplex, white, Light Buff to Pinkish Buff, upper layer soft and cottony, lower layer hard and horny when dry, 0.3–1.5 cm. thick, cottony layer made up of loosely arranged, branching, straight, thick-walled hyphae 4–5 μ in diameter, horny layer of densely arranged, branching, interwoven, undulating, thin-walled hyphae 4–5 μ in diameter; large and conspicuous clamp connections are abundant in both regions of the context; tubes 1–4 mm. long; mouths white, Salmon Buff to Buff Pink, slightly angular, sometimes irregular, averaging 2 per mm.; dissepiments thin, entire or dentate, 100–250 μ thick; hymenium somewhat incrusted, incrustation dissolving in KOH solution; basidia 4–6(8) μ broad, projecting 0–12 μ beyond the general level of the hymenium, sterigmata 2–4 μ long; spores cylindric, straight or allantoid, smooth, hyaline, 6–8 μ x 1–1.5 μ, abundant; hyphal pegs present, composed of from 2 to 3 to 10 or more hyphae arranged parallel or interwoven, projecting 25–35 μ above the level of the hymenium.

Habitat; dead coniferous wood, especially *Picea Engelmanni.*

Distribution: montane and subalpine zones. Found mainly in the Rocky Mountain region and the western Coastal Ranges.

Occurrence: common. Throughout the year.

Type of rot: white rot.

This fungus is very common in the moist Engelmann spruce belt, and occasional specimens may be found at lower elevations. The margin of the pileus is usually inflexed, and at times it almost encloses the tube-layer. The fructifications are usually effused-reflexed, in which case the effused area is greater than the reflexed area; less frequently the growth-form is sessile.

2. Cystidia present, no hyphal pegs or setae.

A. Cystidia with globose incrusted apexes.

a. Spores cylindric-ellipsoid, 7–9 μ long.

6. **Polyporus abietinus** (Dicks.) Fries, Syst. Myc. **1:** 370. 1821.
Boletus abietinus Dicks. Pl. Crypt. Brit. **3:** 21. 1793.
Boletus incarnatus Schum. Enum. Pl. Saell. **2:** 391. 1803.
Polyporus parvulus Schw. Trans. Am. Phil. Soc. II. **4:** 157. 1832.
Coriolus abietinus (Dicks.) Quél. Ench. Fung. p. 175. 1886.
Polystictus pusio Sacc. & Cub. in Sacc. Syll. Fung. **6:** 265. 1888.
Polystictus abietinus Sacc. & Cub. *ibid.*
Daedalea unicolor violacea Clements, Crypt. Form. Colo. *no. 170.* 1905.
Lenzites abietis Lloyd, Mycol. Notes **6:** 909. *f. 1607.* 1920.

Plate 18, figs. 2–6.

Pileus thin, coriaceous, tough, sessile or effused-reflexed, dimidiate, 0.5–4 x 1–5 x 0.1–0.2 cm., effused part up to 8 x 10 cm., sometimes entirely resupinate; surface zonate, villous, strigose, white, Vinaceous-Buff, Avellaneous to Light Drab, often greenish due to the presence of algae; margin thin, continuous, undulating or lobed; context very thin, less than 1 mm., darker than either the pubescence or the tubes, Russet to Mikado Brown, hyphae of the context golden to brownish under the microscope, unbranched, 2–3 μ in diameter; tubes 0.5–7 mm. long, straight or oblique, drying brittle; mouths Livid Purple, Vinaceous-Fawn to Warm Blackish-Brown, purplish in young living plants, light brown in older ones, averaging 2–3 per mm. in poroid forms, round or angular, sometimes decidedly lamellate; dissepiments soon becoming lacerate, 80–150 μ thick, trama golden under the microscope; hymenium 20 μ thick, hyaline; basidia 5–7 μ broad; spores cylindric, elongate-ellipsoid to allantoid, smooth, hyaline, 7–9 x 2–3 μ; cystidia abundant or inconspicuous, hyaline, incrusted or smooth at their apexes, 5–7 μ in diameter, even with the hymenium or projecting up to 15 μ.

Habitat: various coniferous hosts; rare on deciduous ones.

Distribution: from the plains zone up to the subalpine zone. Widespread in the United States.

Occurrence: very common. Found throughout the year.

Type of rot: white rot.

Polyporus abietinus, *P. pargamenus*, and *P. subchartaceus* are closely related species which at times are difficult to separate. When young, all three species have purple-colored hymenia and continuous dissepiments. With age, however, the hymenia turn yellowish-brown in color and the dissepiments become lacerate. Furthermore, the microscopical characteristics of the hymenia of these three species are similar. *Polyporus subchartaceus* is by far the largest, thickest, and most massive plant of the three, and it can be separated on these grounds. *Polyporus abietinus* is usually found growing on conifers, whereas *P. pargamenus* usually occurs on deciduous hosts; but either species is known to occur on both coniferous and deciduous hosts. Separation based on their respective growth-forms seems to be the most logical procedure. *Polyporus abietinus* rarely exceeds 3 cm. in length, whereas *P. pargamenus* is larger, reaching 7 cm. Furthermore, the latter species is usually fan-shaped and attached to the substratum by a narrow, somewhat stalk-like attenuation, whereas the former species does not have this character; its fruiting-bodies may be somewhat fan-shaped, but the place of attachment is broader and never stalk-like.

Some taxonomists consider the lamellate form of *P. abietinus* to be a distinct species. Since in both the poroid and lamellate forms the microscopical characteristics, the host relations, and the macroscopical characteristics other than the pores, are similar, at the present time it seems advisable to consider both forms in the same species.

Polyporus abietinus is one of the first fungi to attack fallen or dead coniferous trees. The fruiting bodies have been observed on trees which have been felled only two months.

7. **Polyporus pargamenus** Fries, Epicr. Myc. p. 480. 1838.
   Polyporus prolificans Fries, *ibid.* p. 443.
   Polyporus laceratus Berk. Ann. & Mag. Nat. Hist. **3**: 392. 1839.
   Polyporus Flabellum Mont. Pl. Cell. Cuba, p. 388, *pl. 15, f. 2.* 1842.
   Polyporus Menandianus Mont. Ann. Sci. Nat. Bot. II. **20**: 362. 1843.

Polyporus subflavus Lév. *ibid.* III. **5**: 300. 1846.
Polyporus xalapensis Berk. & Curt. Jour. Bot. & Kew Misc. **1**: 103. 1849.
Polyporus Sartwellii Berk. & Curt. Grevillea **1**: 51. 1872.
Polyporus ilicincola Berk. & Curt. *ibid.* 52.
Polyporus pseudopargamenus Thuem. Myc. Univ. *no. 1102.* 1878.
Polystictus pargamenus (*pergamenus*) (Fr.) Sacc. Syll. Fung. **6**: 242. 1888.
Coriolus pargamenus (Fr.) Pat. Ess. Tax. Hymen. p. 94. 1900.
Coriolus prolificans (Fr.) Murr. N. Am. Fl. **9**: 27. 1907.

Plate 16, fig. 4.

Pileus thin, coriaceous, sessile, sometimes effused-reflexed, conchate, often narrow at the base and attached by a stalk-like attenuation, 1–7 x 1–7 x 0.1–0.3 cm.; surface zonate, villous or velvety-tomentose, white, Vinaceous Buff, Avellaneous, or Light Drab; margin thin, acute, continuous, undulated, or lobed; context very thin, 1 mm. or less, white to Buckthorn Brown, hyphae of the context hyaline to yellowish under the microscope, branched, 4–6 μ in diameter; tubes 0.5–7 mm. long, drying brittle; mouths varying in color from Livid Purple, Vinaceous Fawn, to Warm Blackish-Brown, purplish in young specimens, brownish in older ones, averaging 2–3 per mm.; dissepiments soon becoming lacerate, 80–150 μ thick; trama hyaline to yellowish under the microscope; hymenium 20 μ thick, hyaline; basidia 5–7 μ broad; spores smooth, hyaline, elongate-ellipsoid to allantoid, 7–9 x 2–3 μ; cystidia abundant or inconspicuous, hyaline, incrusted or smooth at their apexes, even with the hymenium or projecting up to 15 μ. Spores, cystidia, and basidia are the same as in *P. abietinus* (pl. 18, fig. 5).

Habitat: mainly on deciduous hosts and rarely found on conifers.

Distribution: from the foothill zone up to the subalpine zone. Widespread in the United States.

Occurrence: rare. Throughout the year.

Type of rot: white rot.

As previously stated (p. 329), this species may be confused

with *P. abietinus.* For additional differences, compare color, thickness, and branching of the hyphae of the context. This fungus, although common in the eastern United States, is rare in the Rocky Mountains, but is replaced by *P. subchartaceus*, which is considered to be a thick form of this species.

Rhoads[45] has studied the biology of this fungus.

8. **Polyporus subchartaceus** (Murr.) Overh. Wash. Univ. Studies **3**: 32. 1915.

Coriolus subchartaceus Murr. N. Am. Fl. **9**: 24. 1907.

Polystictus subchartaceus (Murr.) Sacc. & Trott. in Sacc. Syll. Fung. **21**: 317. 1912.

Plate 18, fig. 1.

Pileus rigid, tough, sessile to slightly effused, dimidiate to conchate, solitary or imbricate, sometimes confluent, 1–5 x 1–10 x 0.5–1 cm.; surface tomentose to strigose, indistinctly or distinctly zonate, white, Seashell Pink, Light Buff, or Mouse Gray; context white to Light Buff, duplex, hard-corky below, spongy above, 2–5 mm. thick, hyphae of the hard-corky context yellowish under the microscope, branched, 4–6 μ in diameter; tubes 2–6 mm. long; mouths round or angular, 2–3 per mm., Livid Violet in young plants, Vinaceous-Buff to Russet-Vinaceous in more mature ones; dissepiments 100–175 μ thick, soon becoming lacerate; trama golden under the microscope; hymenium 16–20 μ thick, hyaline; basidia 4–6 μ broad, level with the hymenium or projecting up to 10 μ; spores cylindric to allantoid, smooth, hyaline, 7–9 x 2–3 μ; cystidia abundant or inconspicuous, hyaline, incrusted or smooth at the apex, projecting up to 15 μ. The spores and cystidia are the same as in *P. abietinus* (pl. 18, fig. 5).

Habitat: deciduous hosts, especially aspen (*Populus tremuloides*) and cottonwoods (*Populus* spp.).

Distribution: from the plains zone up to the subalpine zone. Known mainly from the Rocky Mountain region.

Occurrence: uncommon. Spring and summer.

Type of rot: white rot.

[45] Rhoads, A. S. N. Y. State Coll. For., Tech. Publ. no. 11. **18**: 1–197. 1918.

Rhoads[46] makes *Polyporus subchartaceus* conspecific with *P. pargamenus*, considering the former species to be a thick form of the latter. The writer, however, prefers to retain *P. subchartaceus*, since it not only has a thicker context, but also a duplex one, and the latter condition does not exist in *P. pargamenus*.

b. Spores ellipsoid, 8–12 μ long.

9. **Polyporus ursinus** Lloyd, Syn. Apus Polyp. p. 319. *f. 650, 660.* 1915.

Plate 19, figs. 5–8.

Pileus spongy, tough, drying horny, dimidiate, effused-reflexed or sessile, solitary or imbricate, 1–6 x 2–12 x 0.5–3 cm.; surface radially appressed-fibrillose to tufted-fibrillose, glabrous with age, azonate, at first whitish or Seashell Pink, turning with age and on bruising to Onion-Skin Pink or Carob Brown; margin thick, rounded, entire, with age undulate, soon glabrous, concolorous to slightly darker; context white to Pale Pinkish Buff, soft, becoming horny on drying, 0.5–2 cm. thick, hyphae of the context closely interwoven, 3–8 μ in diameter, nodose, branched; tubes 1–6 cm. long; mouths Pale Ochraceous-Salmon, Army Brown to Natal Brown, angular, sinuate, irregular, averaging 1–2 per mm.; dissepiments 120–160 μ thick, slightly lacerate with age; hymenium 20–25 μ thick, loosely arranged; basidia 5–8 μ broad, projecting 0–5 μ above the level of the hymenium; spores ellipsoid, smooth, hyaline, 8–12 x 3.5–4.5 μ; cystidia present and numerous, cylindric (4)5–7 μ in diameter, projecting up to 30 μ, with age becoming incrusted at their apexes.

Habitat: various decorticated conifers.

Distribution: montane and subalpine zones. Coniferous regions of the United States.

Occurrence: common. Summer and autumn.

Type of rot: white rot.

Fresh specimens of this species seem unusually heavy when compared with fresh specimens of other pore fungi. When growing under suitable environmental conditions, young specimens contain so much water that when they are squeezed in the hand

[46] Rhoads, A. S. *l.c.* p. 36.

many drops of liquid may be expressed. Consequently the plant shrinks very much on drying. If the fresh plants are bruised or handled they immediately turn reddish-brown in color. A similar color-change is also recorded for *Polyporus fragilis.*

B. Cystidia long and hyphae-like.

10. Polyporus alboluteus Ellis & Ev. Bull. Torr. Bot. Club **25:** 513. 1898.

Fomes alboluteus Ellis & Ev. Proc. Acad. Phila. **1895:** 413. 1895.

Aurantiporellus alboluteus (Ellis & Ev.) Murr. Bull. Torr. Bot. Club **32:** 486. 1905.

Plate 19, figs. 1–4.

Sporophores soft, spongy, effused, occasionally narrowly reflexed, most frequently entirely resupinate, reflexed portion dimidiate, 0.5–4 x 3–15 x 1–5 cm., resupinate portion 5–50 x 5–100 cm. or more, easily separable from the substrata in long flexuous sheets; surface velvety, azonate, Orange Rufus to Stanford's Brown, sometimes becoming incrusted with age and turning black, or bleaching to almost white; context soft, spongy, homogeneous, Salmon-Orange, Orange Chrome to Orange Rufus, 0.1–3 cm. thick, composed of loosely arranged, thick-walled, branched hyphae 4–10 μ in diameter; viewed under the microscope the hyphae appear golden when mounted in water and reddish-brown when mounted in KOH solution; tubes 1–3 cm. long, concolorous, straight or oblique, drying brittle; mouths Orange Pink to Salmon Orange or darker, sometimes turning black when bruised, 1–3 mm. or more broad, angular, becoming lacerate with age; dissepiments thick, 200–600 μ; hymenium yellowish to pinkish under the microscope, 40–60 μ thick; spores elongate-ellipsoid, often apiculate, smooth, hyaline, 9–12 x 3–5 μ; cystidia abundant, hyaline, cylindric, 7–9 μ in diameter, often collapsed, projecting up to 60 μ.

Habitat: on decorticated logs of various conifers, especially *Picea Engelmanni.*

Distribution: montane and subalpine zones. Rocky Mountains and western Coastal Ranges.

Occurrence: common. Spring and summer.
Type of rot: white rot.

This fungus is usually found in a resupinate condition on the under side of decorticated Engelmann spruce logs. Occasionally, sporophores may extend up the side of the log and their margins become narrowly reflexed. This reflexed portion represents the extent of the pileus. The fungus separates easily from the substratum, and large sheets may be stripped off, often one meter or more in length. The walls of the pores soon break down into teeth, and in this stage the fungus may be mistaken for a species of *Irpex* of the Hydnaceae.

The fruiting-bodies of *Polyporus alboluteus*, *P. fibrillosus*, and *P. cinnabarinus* are all red or reddish in color. They can be conveniently separated from one another by the size of their pores: *P. alboluteus* has pores 1–3 mm. broad, *P. fibrillosus* has pores 1–2 per mm., and *P. cinnabarinus* has pores 2–4 per mm.

11. Polyporus fibrillosus Karst. Sydv. Finl. Polyp. p. 30. 1859.
Polyporus aurantiacus Peck, Ann. Rept. N. Y. State Mus. **26:** 69. 1874.
Inonotus fibrillosus Karst. Bidr. Finl. Nat. Folk **37:** 72. 1882.
Polyporus Shiraianus P. Henn. Bot. Jahrb. **28:** 269. 1900.
Pycnoporellus fibrillosus (Karst.) Murr. Bull. Torr. Bot. Club **32:** 489. 1905.

Plate 17, figs. 4–5.

Pileus soft and spongy when fresh, fragile when dry, sessile, dimidiate, imbricate, 3–6 x 4–10 x 0.5–2 cm.; surface fibrillose, zonate, Brazil Red to Vinaceous-Rufus; context spongy-friable when dry, sodden when wet, indistinctly zonate, concolorous with the surface of the pileus or slightly lighter, 0.5–1.5 cm. thick, hyphae of the context turning red in KOH solution and appearing pinkish under the microscope, branched, undulating, 7–10 μ in diameter; tubes 2–6 mm. long; mouths Brazil Brown, fading with age to Light Salmon-Orange or lighter, angular and unequal, 1–2 per mm.; dissepiments becoming lacerate with age, 125–175 μ thick, red-colored in KOH solution, pinkish under the microscope; hymenium 20–30 μ thick, compact; basidia 4–6 μ broad, 4-spored;

spores hyaline, smooth, elongate-ellipsoid, sometimes apiculate, 5–7 x 3–4 μ; hair-like cystidia abundant, hyaline, cylindric, 4 μ in diameter and projecting up to 60 μ beyond the hymenium.

Habitat: coniferous hosts; rare on *Betula*.

Distribution: Pagosa Springs, Colorado. Northern United States.

Occurrence: rare.

Type of rot: brown rot.

The only known collection of this fungus from Colorado was made by Bethel, in 1897, at Pagosa Springs, Colorado. It is a rare fungus throughout the United States.

Polyporus fibrillosus differs from *P. alboluteus* mainly in that the former species has smaller pores.

C. Cystidia ventricose, often buried in the hymenium and rare.

12. Polyporus borealis Fries, Syst. Myc. **1:** 366. 1821.
Spongipellis borealis (Fr.) Pat. Ess. Tax. Hymen. p. 84. 1900.

Plate 20.

Pileus sodden when fresh, drying friable to rigid, dimidiate or substipitate with an attenuated base, 3–12 x 4–20 x 1–4 cm.; surface hispid to tomentose, spongy, azonate, white to Light Ochraceous-Buff or Apricot Buff; margin thin, entire, concolorous; context duplex, fibrous next to the hymenium, soft and floccose above, concolorous with the surface, 0.5–2.5 cm. thick, hyphae of the context branched, undulating, hyaline, 4–7 μ in diameter; tubes 3–12 mm. long, often collapsed in dried specimens; mouths white to Orange-Buff, at first round, later angular or daedaloid, 1–3 per mm.; dissepiments becoming lacerate with age, 120–200 μ thick; hymenium 20–30 μ thick, closely compact; basidia 4–7 μ broad; spores ovoid, sometimes apiculate, smooth, hyaline, 6–8 x 4–5 μ; cystidia abundant or rare, projecting or entirely buried in the hymenium, ventricose, 25–35 x 8–15 μ.

Habitat: on conifers.

Distribution: foothill and montane zones. Eastern and central United States.

Occurrence: rare.

Type of rot: white rot.

Polyporus borealis is of rare occurrence in Colorado as well as throughout the United States. Overholts collected it at Tolland, Colorado, and Bethel made a fine collection in Boulder Canyon, near Boulder, Colorado.

The ventricose cystidia distinctly mark this plant. These cystidia, however, are rarely found in great abundance; and when present, they are often partially or wholly buried in the hymenium.

3. Setae present, often rare or absent; no hyphal pegs or cystidia.

13. Polyporus Rheades (Pers.) Fries, Hym. Eur. p. 551. 1874.

Boletus Rheades Pers. Myc. Eur. **2:** 69. 1825.

Polyporus dryophilus Berk. Lond. Jour. Bot. **6:** 321. 1847.

Polyporus corruscans Fries in Vet. Akad. Forhandl. p. 52. 1851.

Inonotus dryophilus (Berk.) Murr. Bull. Torr. Bot. Club **31:** 597. 1904.

Plate 21, figs. 5–6.

Sporophores thick, subglobose or ungulate, often imbricate, 2–12 x 3–20 x 1.5–10 cm.; surface brown or reddish-brown, as Mahogany Red to Chestnut in the Colorado specimens growing on *Populus* spp., at first fibrillose, then scabrous, finally almost glabrous, zonate or azonate; margin thick, usually obtuse, sterile below; context 1–9 cm. thick, Chestnut-Brown in Colorado plants, zonate, soft when fresh, drying hard and fragile, containing a large central globose granular core which is permeated with white mycelial strands, hyphae of the context dark brown under the microscope, sparingly branched, 4–6 μ in diameter; tubes 2–20 mm. long, concolorous with the context; mouths angular and unequal, averaging 2 per mm., usually concolorous with the context; dissepiments becoming slightly lacerate, 50–120 μ thick; hymenium 9–12 μ thick, hyaline to yellowish or brownish, loosely arranged; basidia 5–8 μ broad, hyaline or yellowish; spores smooth, brownish, ovoid to subglobose, 5–7 x 4.5–5 μ; setae rare or absent (not observed in the Colorado collection), brown, sharply pointed, projecting up to 20 μ.

Habitat: various living and dead deciduous trees, especially species of *Quercus* and *Populus*.

Distribution: montane zone. Widespread in the United States.
Occurrence: rare.
Type of rot: brown heart-rot.

The only known record of the occurrence of this fungus in Colorado is a collection made by E. Smith at Estes Park, Colorado, on *Populus tremuloides.* On aspen, the fungus is imbricate, smaller, and of a darker reddish-brown color than when found growing on species of *Quercus.* Furthermore, the aspen form is not usually zonate. The Colorado collection agrees well with Lloyd's illustration.[47]

The hard central globose core, which is usually interwoven with white mycelial strands and is of a more granular consistency than the rest of the context, distinctly marks this species.

4. No hyphal pegs, cystidia, or setae present in the hymenium.
A. Spores allantoid, 2 μ or less in thickness.

14. Polyporus caesius (Schrad.) Fries, Syst. Myc. **1**: 360. 1821.
Boletus caesius Schrad. Spic. Fl. Germ. p. 167. 1794.
Boletus albidus Sow. Col. Figs. Eng. Fung. *pl. 226.* 1799.
Tyromyces caesius (Schrad.) Murr. N. Am. Fl. **9**: 34. 1907.

Plate 28, fig. 3.

Pileus sessile, rarely effused-reflexed, dimidiate, soft and spongy, fresh plants turn blue where touched or bruised, 1–5 x 1–6 x 0.5–2 cm.; surface sodden, tomentose to villous, azonate, white, Mineral Gray to Light Buff; context white, friable and soft, 3–15 mm. thick, hyphae of the context sparingly branched, 5–7 μ in diameter; tubes 2–9 mm. long, collapsing on drying; mouths white, Mineral Gray to Pinkish-Buff, angular, 3–4 per mm.; dissepiments 40–80 μ thick, lacerate with age; hymenium hyaline, 12–15 μ thick; basidia 4–6 μ broad; spores oblong-allantoid, hyaline, 3–5 x 1–1.5 μ; cystidia none.
Habitat: on both deciduous and coniferous hosts.
Distribution: montane zone. Widespread in the United States.
Occurrence: rare.
Type of rot: white rot.

Polyporus caesius is of common occurrence in many parts of

[47] Lloyd, C. G. Mycological Writings **5**: 755. *f. 1129.* 1916.

the United States, but in the Rocky Mountains it is extremely rare. The only known Colorado collection was made by Kauffman at Tolland, Colorado, on well-rotted coniferous logs. This species is the only soft, white-colored polypore that turns blue when touched or bruised.

15. **Polyporus resinosus** (Schrad.) Fries, Syst. Myc. **1**: 361. 1821. Not *P. resinosus* Rostk. 1838.

Boletus fuliginosus Scop. Fl. Carn. ed. 2. **2**: 470. 1772.
Boletus resinosus Schrad. Spic. Fl. Germ. p. 171. 1794.
Boletus benzoinus Wahlenb. Fl. Suec. **2**: 1076. 1826.
Polyporus benzoinus (Wahlenb.) Fries, Elench. Fung. p. 100. 1828.
Polyporus fuliginosus (Scop.) Fries, Epicr. Myc. p. 451. 1838.
Trametes benzoina (Wahlenb.) Fries, *ibid.* p. 489.
Ischnoderma resinosum (Schrad.) Karst. Medd. Soc. Faun. Fl. Fenn. **5**: 38. 1879.
Fomes fuliginosus (Scop.) Sacc. Syll. Fung. **6**: 164. 1888.
Ungulina fuliginosa (Scop.) Pat. Ess. Tax. Hymen. p. 103. 1900.
Ischnoderma fuliginosum (Scop.) Murr. Bull. Torr. Bot. Club **31**: 606. 1904.

Plate 22, fig. 2.

Pileus fleshy when fresh and with an anise-like odor, drying rigid, imbricate, sessile, effused-reflexed or entirely resupinate, applanate or dimidiate, sometimes affluent, 5–15 x 6–30 x 0.5–2.5 cm.; surface becoming pelliculose, rugose, zonate in mature plants, drying Snuff Brown, Prout's Brown to Bister, some zones blackish; context fleshy in fresh plants, drying firm and fragile, 3–15 mm. thick, Light Ochraceous-Buff to Tawny-Olive, hyphae of the context yellowish-brown under the microscope, sparingly branched, undulating, thick-walled, 5–7 μ in diameter; tubes 1–8 mm. long; mouths Light Buff to Cinnamon-Buff, darker (Sayal Brown to Warm Sepia) when bruised and on drying, round to angular, averaging 4–6 per mm.; dissepiments yellowish-brown under the microscope, 60–160 μ thick; hymenium usually loosely arranged, apparently absent in old specimens; basidia hyaline, 3–5 μ in

diameter; spores smooth, hyaline, allantoid, 5–7 x 1–2 μ; no cystidia or setae.

Habitat: various deciduous and coniferous hosts.

Occurrence: rare. Autumn.

Distribution: montane zone. Widespread in the United States.

Type of rot: white rot.

In the old sense, *Polyporus resinosus* grows only upon deciduous hosts, whereas *P. benzoinus,* which is evidently the same plant, grows only upon coniferous hosts. Snell *et al*[43] have pointed out that the cultural characteristics for the two plants mentioned above are quite similar. For the present, these two species are considered as conspecific.

B. Spores elongate-ellipsoid to cylindric, rarely allantoid, 1.5–3.5 μ in thickness.

16. Polyporus adustus (Willd.) Fries, Syst. Myc. **1**: 363. 1821.
Boletus adustus Willd. Fl. Berol. p. 392. 1787.
Boletus fuscoporus Planer, Ind. Pl. Erf. p. 26. 1788.
Boletus suberosus flabelliformis Batsch, Elench. Fung. Contin. **2**: 117. *pl. 226.* 1789.
Boletus pelleporus Bull. Herb. Fr. *pl. 501, f. 2.* 1790.
Boletus carpineus Sow. Col. Figs. Eng. Fung. *pl. 231.* 1799.
Polyporus pallescens Fries, Syst. Myc. **1**: 369. 1821.
Boletus isabellinus Schw. Schr. Nat. Ges. Leipzig **1**: 96. 1822.
Polyporus subcinereus Berk. Ann. & Mag. Nat. Hist. **3**: 391. 1839.
Bjerkandera adusta (Willd.) Karst. Medd. Soc. Faun. Fl. Fenn. **5**: 38. 1879. In part.
Myriadoporus adustus (Willd.) Peck, Bull. Torr. Bot. Club **11**: 27. 1884.

Plate 21, figs. 1–4.

Pilei fleshy-tough, drying brittle, conchate, sessile or effused-reflexed, imbricate, sometimes confluent, 1–5 x 2–10 x 0.1–0.8 cm.; surface sometimes undulate, indistinctly zonate or azonate, tomentose, white, Pink Buff, Warm Buff, Light Pinkish Cinna-

[43] Snell, W. H., W. G. Hutchinson, and K. H. N. Newton, Mycologia **20**: 279–280. 1928.

mon to Pale Smoke Gray; margin thin, acute, even to undulate, sterile below, often blackish in dried plants; context corky, white to Light Buff, 1–7 mm. thick, hyphae radially arranged, hyaline, rarely branched, thick-walled, 5–7 μ in diameter; tubes 0.5–4 mm. long; mouths various shades of smoke-color to black, very small, 4–6 per mm., round to angular, in dried plants the tubes sometimes become tufted; dissepiments thin, 50–100 μ; trama brownish under the microscope; hymenium hyaline, 7–9 μ thick; basidia 4-spored, 4–5 μ broad; spores hyaline, smooth, oblong to elongate-ellipsoid, rarely allantoid, 3–5 x 1.5–2.5 μ; cystidia none.

Habitat: deciduous hosts, especially species of *Populus;* rare on conifers.

Distribution: from the plains zone up to the subalpine zone. Widespread in the United States.

Occurrence: very common. Spring and summer.

Type of rot: spongy white rot.

Polyporus adustus is very commonly found on cottonwood (*Populus* spp.) stumps and logs on the plains and in the foothills; higher up, it is found on *Populus tremuloides.* Overholts collected this species of fungus on pine at Tolland, Colorado.

Three species of pore fungi having smoke-colored hymenia occur in the state of Colorado: *Polyporus adustus*, *P. crispus*, and occasionally *P. hirsutus.* In the latter species, the hymenium is white or very light smoke-colored and it never turns blackish as in the two former species. *Polyporus adustus* and *P. crispus* are more difficult to separate. The latter species is usually larger and the pileus is covered with radially adpressed, long, stiff fibrils; also, the latter species occurs more densely imbricated and the margin of the pileus is more crisped and wavy than in the former.

17. Polyporus crispus (Pers.) Fries, Obs. Myc. **1**: 127. 1815; Syst. Myc. **1**: 363. 1821.

Boletus adustus crispus Pers. Obs. Myc. **2**: 8. 1799.

Boletus crispus Pers. Syn. Fung. **2**: 529. 1801.

Bjerkandera adusta (Willd.) Karst. Medd. Soc. Faun. Fl. Fenn. **5**: 38. 1879. In part.

Plate 23, fig. 1.

Pilei fleshy-tough, drying brittle, conchate, sessile or effused-reflexed, densely imbricate, 1–8 x 3–10 x 0.1–0.5 cm.; surface undulate, zonate or azonate, radially adpressed-fibrillose, usually strigose at the base, color-range from Light Buff to Clay Color; margin thin, acute, crisped or wavy, frequently blackish, sterile below; context corky, white to Light Buff, 1–4 mm. thick, hyphae radially arranged, hyaline, rarely branched, thick-walled, 5–7 μ in diameter; tubes 0.5–4 mm. long; mouths various shades of smoke-color to black, very small, 4–6 per mm., round; dissepiments 90–120 μ thick; trama brownish under the microscope; hymenium hyaline, 7–9 μ thick; basidia 4-spored, 4–5 μ broad; spores hyaline, smooth, oblong to elongate-ellipsoid, rarely allantoid, 3–5 x 1.5–2.5 μ; cystidia none.

Habitat: on *Populus tremuloides* and probably other deciduous hosts; reported on pine.

Distribution: foothill and subalpine zones. Widespread in the United States.

Occurrence: rare.

Type of rot: spongy white rot.

Polyporus crispus is very closely related to *P. adustus.* The former differs from the latter chiefly in the radially adpressed fibrils on the surface of the pileus, more dense imbrication, and more wavy margin.

18. **Polyporus fragilis** Fries, Elench. Fung. p. 86. 1828.
Spongipellis fragilis (Fr.) Murr. Southern Polyp. p. 61. 1915.

Plate 24, fig. 4.

Pileus fleshy, becoming hard and fragile when dry, sessile or effused-reflexed, plano-depressed, reniform, dimidiate, sometimes attenuated behind into a stem-like base, and pendulous, imbricate, 3–7 x 3–7 x 0.5–1 cm.; surface azonate, or in mature plants indistinctly zonate, villose, rugose, whitish, becoming brown-spotted where touched, drying Hazel, Chestnut, to Chestnut-Brown; margin thin, fragile, concolorous; context 2–10 mm. thick, radially fibroid, drying hard and fragile, Pinkish Buff to Ochraceous-Tawny, hyphae of the context yellow under the microscope, nodose-septate, branched, of various diameters, 3–8 μ; tubes 2–8

mm. long, whitish, becoming Pinkish Buff, Carob Brown to Russet on drying; mouths whitish, becoming brown-spotted where touched, drying concolorous with the tubes, round or angular, becoming sinuous and labyrinthiform, 3–4 per mm.; dissepiments 75–100 μ thick, occasionally containing diamond-shaped crystalline bodies, 20 x 15 μ; hymenium hyaline, 10–12 μ thick; basidia hyaline, 9–10 x 5 μ, 4-spored; spores smooth, hyaline, cylindric, occasionally allantoid, 4–6 x 1.5–2 μ; no cystidia observed.

Habitat: on coniferous hosts.

Distribution: montane and subalpine zones. Widespread in the United States throughout the coniferous regions.

Occurrence: rare.

Type of rot: brown rot.

Fresh and young specimens of *Polyporus ursinus*, *P. fragilis*, and *P. mollis* all become brown-spotted where bruised or touched and some care must be exercised in separating these species. The latter species, however, has not as yet been reported from Colorado; *P. ursinus* can be separated on the presence of incrusted cystidia in its hymenium.

Polyporus fragilis is rare throughout the world, and only three collections have been reported from Colorado. The above description has been drawn from a collection made by Kauffman at Tolland, Colorado, in 1920.

19. **Polyporus cinnabarinus** (Jacq.) Fries, Syst. Myc. **1**: 371. 1821.

Boletus cinnabarinus Jacq. Fl. Austr. **4**: 2. 1776.

Boletus coccineus Bull. Herb. Fr. p. 364. 1791.

Trametes cinnabarina (Jacq.) Fries, Nov. Symb. p. 98. 1851.

Polystictus cinnabarinus (Jacq.) Sacc. Syll. Fung. **6**: 245. 1888.

Pycnoporus cinnabarinus (Jacq.) Karst. Rev. Myc. **3**[9]: 18. 1881.

Plate 24, fig. 1.

Pileus tough-leathery to rigid, sessile, dimidiate or flabelliform, 1–10 x 1–20 x 0.5–2 cm. (Colorado plants 1–5 x 1–5 x 0.5–1 cm.); surface azonate, rugulose, tomentose to glabrous, Etruscan Red,

Cinnamon-Rufus to Flame Scarlet, fading to Salmon Buff or white; margin thin and acute; context floccose, zonate, concolorous with the surface of the pileus, 1–15 mm. thick, hyphae of the context thick-walled, sparingly branched, yellowish under the microscope, 4–8 μ in diameter; tubes 1–5 mm. long; mouths circular to angular, 2–4 per mm., Brazil Red to Morocco Red; dissepiments yellowish under the microscope, 50–200 μ thick; hymenium yellowish to almost hyaline, 8–10 μ thick; basidia 6–7 μ broad; spores hyaline to yellowish, cylindric, rarely curved, smooth, 5–7 x 2–3 μ; cystidia none.

Habitat: on birch (*Betula* spp.), poplar (*Populus* spp.), and aspen (*Populus tremuloides*); rare on coniferous hosts.

Distribution: foothill zone. Widespread in the United States.

Occurrence: uncommon. Spring and summer.

Type of rot: white rot.

This fungus, although common in the eastern and central United States, has been collected only a few times in Colorado. Its color, however, is so obvious that the species may be recognized at once.

20. Polyporus anceps Peck, Bull. Torr. Bot. Club **22**: 207. 1895.

Tyromyces Ellisianus Murr. N. Am. Fl. **9**: 34. 1907.
Tyromyces anceps (Pk.) Murr. *ibid.* 35.
Polyporus Ellisianus (Murr.) Sacc. & Trott. in Sacc. Syll. Fung. **21**: 281. 1912.

Plate 23, fig. 2.

Pileus effused-reflexed, reflexed portion narrow, dimidiate, imbricate, frequently entirely resupinate, laterally connate, subcorky, drying rigid, 0.5–3 x 2–10 x 0.3–1.5 cm.; surface azonate to indistinctly zonate, minutely downy to scabrous, sometimes rugosely pitted, whitish to cream-color, drying Cream-Buff, Warm Buff, to Pinkish Buff; margin abrupt, concolorous or slightly darker where bruised, even or undulating; context white, drying white to Light Buff, 2–6 mm. thick, composed of hyphal complexes in which the individual hyphae vary from 1 to 7 μ in diameter, smaller branches interwoven and occasionally incrusted with

yellow crystalline material that is partially soluble in KOH solution; tubes 3–10 mm. long, often oblique, white, Pinkish Buff to Warm Buff; mouths concolorous, darker where bruised, circular to angular, 3–5 per mm.; dissepiments 60–120 μ thick; hymenium hyaline, thin, 16–20 μ broad; basidia hyaline, 5–6 μ broad; spores hyaline, smooth, cylindric to elongate-ellipsoid, rarely curved, 7–9 x 3–3.5 μ; no cystidia.

Habitat: on various coniferous hosts.

Distribution: foothill zone. Coniferous regions of the United States except the far west.

Occurrence: very rare. Summer and autumn.

Type of rot: white pocket rot.

The one outstanding character of *Polyporus anceps* is the hyphal complex nature of the context. These complexes have thick central axes with thinner and tapered side-branches coming off in a dendroid fashion.

This species is apparently rare in the Rocky Mountain region, and at the present time only a single collection from Colorado has been recorded.

C. Spores ellipsoid to subglobose, 4–5 μ in thickness.

21. Polyporus planellus (Murr.) Overh. Wash. Univ. Studies **3:** 29. 1915.

Polyporus planus Peck, Ann. Rept. N. Y. State Mus. **31:** 37. 1879. Not *P. planus* Wallr. 1833.

Coriolus planellus Murr. Bull. Torr. Bot. Club **32:** 649. 1906.

Plate 22, fig. 1.

Pileus thin, coriaceous-rigid, dimidiate or flabelliform, sometimes narrowly attached, sessile, effused-reflexed or entirely resupinate, 1–3.5 x 1–4 x 0.05–0.2 cm.; surface tomentose when young, becoming glabrous, rugulose, multizonate with occasional intermixed dark or blackish zones, Auburn, Raw Umber, Chestnut-Brown, or lighter; margin very thin, undulating to lobed, usually lighter-colored to almost white, sterile below; context less than 1 mm. thick, Light Pinkish Cinnamon, hyphae of the context brownish under the microscope, branched, 3–4 μ in

diameter; tubes less than 1 mm. long; dissepiments entire, brownish under the microscope, 40–100 μ thick; mouths angular to daedaloid, 5–6 per mm., white, Vinaceous-Buff to Vinaceous-Pink; hymenium hyaline, 16–20 μ thick; basidia 6–8 μ broad, 4-spored; spores hyaline, smooth, ovoid to ellipsoid, 9–12 x 4 μ; no cystidia observed.

Habitat: various deciduous hosts.

Distribution: foothill and montane zones. Found throughout the northern part of the United States.

Occurrence: rare. Summer.

Type of rot: unknown.

This fungus differs from *Polyporus versicolor* in having a brownish-colored context and trama, in having larger and different shaped spores, and in the absence of hyphal pegs. *Polyporus planellus* is almost always resupinate; occasionally, the margin is narrowly reflexed, and rarely is it found to be sessile.

22. Polyporus spumeus (Sow.) Fries, Syst. Myc. **1**: 358. 1821.

Boletus spumeus Sow. Col. Figs. Eng. Fung. *pl. 211*. 1797.
Spongipellus spumeus (Sow.) Pat. Ess. Tax. Hymen. Eur. **1**: 140. 1887.
Spongipellus occidentalis Murr. N. Am. Fl. **9**: 38. 1907.

Plate 28, fig. 2.

Pileus soft and watery and with an anise-like odor when fresh, drying rigid, dimidiate, sessile, subimbricate, rarely attenuated towards the base into a stalk-like process, convex above, 5–20 x 6–20 x 2–6 cm., much thinner when dry; surface azonate, hirsute, fibrillose, or matted-strigose, white to yellowish, drying Light Ochraceous-Buff, Ochraceous-Buff to Ochraceous-Tawny; margin acute, undulating to lobed, concolorous; context in fresh plants white to yellowish, drying Cinnamon-Buff to Clay Color, indistinctly duplex, soft and cottony above, firm and fibrous next to the tubes, 1–3 cm. thick, hyphae of the context partially gelatinized, hyaline, branched, 3–6 μ in diameter; tubes concolorous with the context, distinct from the context but not separable, 0.5–3 cm. long, when dry often collapsed; mouths angular, con-

colorous or drying as dark as Hazel, 2–4 per mm.; dissepiments with age becoming dentate-lacerate, 60–120 μ broad; hymenium hyaline, 18–22 μ broad; basidia hyaline, 5–7 μ in diameter; spores hyaline, smooth, ellipsoid to subglobose, apiculate, 5–7 x 4–5 μ; no cystidia.

Habitat: cottonwoods (*Populus* spp.) and other deciduous hosts.

Distribution: plains zone. Northern United States.

Occurrence: rare. Summer.

Type of rot: white rot (?).

The only known collection of this fungus from Colorado was made by Bethel, at Denver, Colorado, on cottonwood. The anise-like odor of the fresh plant is a noteworthy characteristic.

The original illustration of this species by Sowerby (*l. c.*) shows the plant to be substipitate, a condition that apparently is not common, and which has led to considerable confusion. The description as given above defines the plant as it is known in America.

Section II. Sporophores centrally, excentrically, or laterally stipitate; all gymnocarpous.

1. Hyphal pegs present; cystidia and setae absent.

23. Polyporus arcularius (Batsch) Fries, Syst. Myc. **1:** 342. 1821.

Boletus arcularius Batsch, Elench. Fung. p. 97. 1783. Not *B. arcularius* Schw. 1822.

Polyporus arculariformis Murr. Torreya **4:** 151. 1904.

Plate 24, figs. 5–6.

Pileus circular, convex to umbilicate, 1–8 cm. in diameter, 1–4 mm. thick; surface azonate, depressed center, squamulose, hispid-tomentose or glabrous, Cinnamon-Buff to Antimony Yellow when fresh, drying Buckthorn Brown to Pecan Brown; margin acute, ciliate, straight, reflexed on drying; context white, drying white to Pinkish Buff, 0.5–2 mm. thick, hyphae of the context hyaline under the microscope, branched, 2–5 μ in diameter; tubes decurrent, white to Pinkish Buff, drying Light Pinkish Buff to Tawny, 1–3 mm. long; mouths large, angular, concolorous with

the tubes, about 1 mm. broad; stipe central, slender, 2–4 cm. long, 2–3 mm. thick, squamulose, hispid-tomentose or glabrous above, fibrillose and bulbous at the base, concolorous with the pileus or slightly darker; dissepiments hyaline under the microscope, 150–250 μ broad, tapered towards the mouths to an acute edge, edges slightly denticulate; hymenium hyaline, closely compact, 16–20 μ broad; basidia 5–7 μ broad; spores hyaline, smooth, elongate-ellipsoid, apiculate, 7–9 x 2–3 μ; hyphal pegs present, usually incrusted, hyphae scarcely discernible, projecting up to 60 μ and 15–20(45) μ in diameter.

Habitat: on various deciduous hosts, especially *Populus tremuloides.*

Distribution: montane zone. Widespread in the United States.

Occurrence: uncommon. Spring and early summer.

Type of rot: white rot.

Polyporus arcularius is characterized by its honey-colored pileus, its ciliate margin, and its large angular pores. *Favolus alveolaris* likewise has large angular pores, but lacks the ciliated margin of the pileus.

2. Cystidia present, rare or at times absent; no hyphal pegs or setae.

24. Polyporus Schweinitzii Fries, Syst. Myc. **1:** 351. 1821.

Boletus sistotremoides Alb. & Schw. Consp. Fung. p. 243. 1805.

Daedalea epigaea Lenz, Schwämme, p. 62. 1831.

Polyporus tabulaeformis Berk. Lond. Jour. Bot. **4:** 302. 1845.

Polyporus spectabilis Fries, Nov. Symb. p. 48. 1851.

Polyporus hispidoides Peck, Ann. Rept. N. Y. State Mus. **33:** 21. 1880.

Polystictus Schweinitzii (Fr.) Karst. Rev. Myc. **3**^{9}: 18. 1881.

Cladomeris Schweinitzii (Fr.) Quél. Ench. Fung. p. 169. 1886.

Phaeolis sistotremoides (Alb. & Schw.) Murr. Bull. Torr. Bot. Club **32:** 363. 1905.

Plate 25, figs. 1–2.

Pileus stipitate, occasionally sessile, convex, umbonate to infundibuliform, spongy and of light weight, variously shaped from

dimidiate to circular, 5–20–50 cm. or more broad, 0.5–2(4) cm. thick; surface azonate to zonate, strigose-tomentose, even, pitted, rugulose or nodulose, Kaiser Brown, Auburn, Bay, or black; margin concolorous or Yellow Ocher, often finely velvety-tomentose, inflexed when dry, sterile below; context soft and spongy, drying fragile-friable, zonate, 0.2–3(6) cm. thick, Raw Sienna, Argus Brown to Chestnut-Brown, hyphae of the context dark-brown under the microscope, often collapsed, branched, 6–12 μ in diameter; tubes decurrent, 2–8 mm. long, Light Orange-Yellow, changing color with age and becoming concolorous with the surface; mouths concolorous with the tubes, irregular and of unequal size, about 1 mm. broad; dissepiments 120–150 μ thick, dentate with age, occasionally breaking down, resulting in pores of extra large size; trama concolorous with the context; stipe central, excentric, lateral or wanting, when present 1–6 cm. long, 1–4 cm. thick, of the same color and structure as the pileus; hymenium yellow, compact, 16–22 μ broad; basidia yellow, 4-spored, 6–8 μ in diameter; spores hyaline, smooth, ovoid-ellipsoid, 6–8 x 4–5 μ; cystidia occasional, rare, or entirely absent, long-cylindric or clavate, yellowish-brown, 8–10 μ broad, projecting up to 60 μ.

Habitat: living or dead conifers; ground near conifers, but apparently attached to their roots. Rare on deciduous trees.

Distribution: throughout the coniferous regions of Colorado and the United States.

Occurrence: uncommon. Summer and autumn.

Type of rot: brown rot.

This fungus is of outstanding economic importance in causing the decay of both living and dead coniferous trees. The sporophores are usually found growing from the buried and aboveground parts of roots; occasionally they are attached to the trunk of the tree, and in this case the fruiting bodies are often sessile. Of the synonyms, *Polyporus tabulaeformis* and *P. hispidoides* refer to the sessile form of growth.

Sections through the pores of this fungus, when examined under the microscope, show a dark-brown trama and a yellowish hymenium. The hymenium likewise appears yellow to yellowish-red to the unaided eye. In old and weathered plants, however, the hymenium becomes concolorous with the trama, and hence

this color-differentiation loses its significance. An orange-yellow alcohol- and water-soluble pigment is present in this fungus.

3. Setae present and abundant; no hyphal pegs or cystidia.

25. **Polyporus circinatus** Fries, Monogr. Hymen. Suec. **2:** 268. 1863.

Polyporus dualis Peck, Ann. Rept. N. Y. State Mus. **30:** 44. 1878.

Coltricia tomentosa (Fr.) Murr. Bull. Torr. Bot. Club **31:** 346. 1904; *Polyporus tomentosus* sensu Murrill.

Polyporus Peakensis Lloyd, Mycol. Notes **6:** 933. 1920.

Plate 26, figs. 1–2.

Pileus circular to flabelliform, convex, plane or depressed at the center, 3–20 cm. in diameter, 3–20 mm. thick, solitary or caespitose, rarely confluent; surface azonate or indistinctly zonate, velvety-tomentose, Mars Yellow to Ochraceous-Tawny; margin acute, usually sterile below, entire or lobed, of a lighter color as: Pale Orange to Warm Buff; context 1–15 mm. thick, duplex, upper part soft-corky, homogeneous and concolorous with the surface, lower part woody, homogeneous or indistinctly multizonate, usually of a lighter color as: Light Orange-Yellow to Ochraceous Buff, hyphae of the two regions of the context apparently similar under the microscope, brownish, undulating, sparingly branched, 5–7 μ in diameter; tubes short-decurrent, 1–5 mm. long, Cinnamon-Buff to Clay Color, usually whitish within; mouths angular, irregular, unequal, 2–3 per mm., concolorous with the tubes or Light Buff; dissepiments becoming dentate with age, tomentose-hairy at the mouths, 120–150 μ thick; stipe central, excentric or lateral, sometimes lacking, unequal, usually obese, of the same structure and color as the pileus, up to 5 cm. long, 0.5–3 cm. thick; hymenium hyaline, 16–20 μ broad; basidia hyaline, small, 4–5 μ broad; spores smooth, hyaline under the microscope, cylindric-ovoid, 4–6 x 3–4 μ; setae pointed, often incrusted and the incrustation soluble in KOH solution, projecting up to 50 μ, 8–12 μ broad at their bases.

Habitat: on the ground in coniferous forests and apparently

attached to buried wood, rarely found in deciduous forests or growing directly attached to wood.

Distribution: montane and subalpine zones. Widespread in the United States.

Occurrence: frequent. Summer and autumn.

Type of rot: white rot.

Polyporus circinatus is most frequently found growing in troops on the ground in coniferous forests. The finer hyphae may be traced to buried wood or roots where it produces a white pocket rot. The soft, brown pileus and the duplex context distinctly separate this fungus from all other stipitate polypores known to occur in Colorado.

Some authors consider *Polyporus tomentosus* Fr. and *P. circinatus* to be synonymous. Lloyd,[49] however, points out that the former has a homogeneous context and is thus distinct. Furthermore, he is of the opinion that it does not occur in the United States. Undoubtedly, all American plants so named belong to *Polyporus circinatus.*

Polyporus Peakensis, which was described by Lloyd from a single specimen collected by Hedgcock, near Moraine Lake, Pikes Peak, Colorado, is conspecific.

Hubert,[50] reports this fungus to be parasitic on pine.

4. No hyphal pegs, cystidia, or setae in the hymenium.

A. Spores ovoid to subglobose, 3–5 x 2–4 μ.

26. **Polyporus ovinus** (Schaeff.) Fries, Syst. Myc. **1**: 346. 1821.
Boletus ovinus Schaeff. Icon. Fung. **2**: *pl. 121, 122.* 1780.
Scutiger ovinus (Schaeff.) Murr. Mycologia **12**: 20. 1920.

Plate 24, fig. 2.

Pilei fleshy, gregarious or solitary, circular, convex, 4–14 cm. in diameter, 3–10 mm. thick; surface at first tomentose, white or tan-colored, with age becoming areolate, subsquamulose, or more rarely subpelliculose, drying Avellaneous to Fawn Color and black-spotted; margin acute, even or undulating, concolorous or

[49] Lloyd, C. G. Synopsis of the stipitate Polyporoids. pp. 159–160. Cincinnati, 1912.

[50] Hubert, E. E. Phytopath. **19**: 745–747. 1929.

blackish, inflexed on drying, sterile below; context at first white, drying Light Pinkish Cinnamon, usually containing a black line adjacent to the tubes, 1–6 mm. thick, hyphae of the context slightly colored under the microscope, walls partially gelatinized, branched, of markedly unequal diameters, varying from 4 up to 25 μ; tubes decurrent, at first whitish, drying Clay Color, Tawny to Chestnut-Brown, 1–3 mm. long; mouths angular, concolorous with the tubes, 2–3 per mm.; dissepiments with age becoming dentate, 20–80 μ broad; trama slightly colored under the microscope; stipe central, solid, usually with a bulbous base, tomentose, at first whitish to tan-colored, drying Light Vinaceous-Cinnamon to Clay Color, often black-spotted, bulbous base Apricot Buff, 2–7 cm. long, 1–2 cm. thick; hymenium hyaline, 12–18 μ broad; basidia hyaline, very small, 3–4 μ in diameter; spores hyaline, smooth, subglobose, 3.5–4.5 x 2.5–3 μ; no cystidia.

Habitat: on the ground in coniferous forests.

Distribution: montane zone. Northern United States.

Occurrence: rare.

Polyporus ovinus is rare in the United States, and is known from Colorado only from the collections of F. E. and E. S. Clements distributed in their "*Cryptogamae Formationum Coloradensium" no. 338*, as *Polyporus subsquamosus*.

In dried plants, the pileus and stipe of this fungus appear "scorched" or blackish-spotted, and the base of the stipe is frequently pinkish, but never as pink as in dried plants of *Polyporus confluens*. The black line at the base of the tubes appears to be a fairly constant character. Additional characters of this species are the small spores and the partially gelatinized hyphae of the context which are of varying diameters.

In Europe, the pileus of this plant may be decidedly squamulose, as is shown in Schaeffer's 'Icones' plate 122, and by *no. 1423* of Sydow's 'Mycotheca Germanica.' The American plants, however, are most like those illustrated by Schaeffer in his plate 121, but at times a more areolated or subsquamose condition of the surface of the pileus may be encountered.

27. Polyporus confluens (Alb. & Schw.) Fries, Syst. Myc. **1:** 355. 1821.

Boletus confluens Alb. & Schw. Consp. Fung. p. 244. 1805.
Not *B. confluens* Schum. 1803.
Scutiger laeticolor Murr. Bull. Torr. Bot. Club **30:** 428. 1903.
Scutiger Whiteae Murr. *ibid.* 432.

Plate 28, fig. 1.

Pilei solitary or gregarious, confluent, circular or irregular, convex or umbilicate, 5–16 cm. in diameter, 1–3 cm. thick; surface glabrous, pelliculose, with age becoming rimose, areolate or scaly, when fresh Ivory-White, Buff-Pink, Cinnamon-Buff to Clay-Color, drying Cinnamon-Buff to Mikado Brown; margin entire to lobed, thin, incurved, concolorous; context 1–2.5 cm. thick, white, soft when fresh, drying Cinnamon-Buff to Buff-Pink, usually containing a thin reddish-orange stratum adjacent to the tubes, hyphae of the context hyaline, gelatinized and not easily discernible, branched, densely interwoven, of various thicknesses, 2–10 μ in diameter; tubes 1–2 mm. long, subdecurrent to long-decurrent, often oblique, white to Cream Color when fresh, changing on drying to Flame Scarlet, Cinnamon-Buff or Buff-Pink; mouths concolorous with the tubes, frequently stuffed, angular, 2–3 per mm.; dissepiments at first thick, with age becoming thin and denticulate, occasionally breaking down, resulting in pores of extra large size; hyphae of the trama gelatinized as in the context; stipe simple, branched or confluent, 3–10 cm. long, 0.5–2 cm. thick, concentric to excentric, round or compressed, solid and homogeneous, usually pointed at the base, concolorous with the pileus; hymenium 16–20 μ broad; basidia 4-spored, 5–6 μ in diameter; spores hyaline, smooth, ovoid to subglobose, apiculate, 4–5 x 3–4 μ; no cystidia.

Habitat: on the ground in coniferous forests.

Distribution: montane and subalpine zones. Northeastern United States.

Occurrence: uncommon. Autumn.

Polyporus confluens, as the specific name implies, is frequently found with both the pilei and the stipes confluent; however, single and well-formed specimens that are not confluent may be found. In fresh plants, the context and the tubes are whitish, but on bruising and on drying they turn pink. In many dried

plants, the tubes and a narrow stratum of the adjacent context are reddish-colored.

Kauffman[51] has fully discussed and well illustrated his Colorado collections of this species.

B. Spores elongate-ellipsoid.

a. Spores 7–9 x 4–5 μ.

28. Polyporus perennis (L.) Fries, Syst. Myc. **1:** 350. 1821.
Boletus perennis L. Sp. Pl. p. 1177. 1753.
Boletus coriaceus Scop. Fl. Carn. ed. 2. **2:** 465. 1772.
Boletus subtomentosus Bolt. Hist. Fung. **2:** 87. *pl. 87.* 1788.
Boletus confluens Schum. Enum. Pl. Saell. **2:** 378. 1803. Not *B. confluens* Alb. & Schw. 1805.
Coltricia connata S. F. Gray, Nat. Arr. Brit. Pl. **1:** 644. 1821.
Polystictus perennis (L.) Karst. Rev. Myc. **3**[9]**:** 18. 1881.
Pelloporus perennis (L.) Quél. Ench. Fung. p. 166. 1886.
Coltricia perennis (L.) Murr. Jour. Myc. **9:** 91. 1903.

Plate 26, fig. 3.

Pilei gregarious, sometimes confluent, coriaceous, thin, circular, convex or umbilicate, 1–6 cm. in diameter, 1–6 mm. thick; surface zonate, tomentose, substriate, the zones sometimes glabrous, Sudan Brown to Hazel, rarely paler and cinereous as Tilleul-Buff; margin thin, acute, even, undulating to lobed, sometimes fimbriate from the extended tomentum, occasionally sterile below; context less than 1 mm. thick, concolorous with the surface, hyphae of the context reddish-brown under the microscope, sometimes collapsed, branched, 6–8 μ in diameter; tubes adnate to decurrent, 1–4 mm. long, grayish within; mouths angular, 2–3 per mm., Ochraceous-Tawny, Sayal Brown to Cinnamon Brown; stipe central, velvety, usually concolorous with the pileus, sometimes broadly attached, occasionally flat and branched, more frequently round and unbranched, solid, rarely stuffed, often bulbous at the base, 2–5 cm. long, 1–10 mm. thick; dissepiments denticulate, 100–150 μ broad, tapered towards the mouths; trama concolorous with the context; hymenium loosely arranged,

[51] Kauffman, C. H. Mich. Acad. Sci. Arts & Lett., Papers **1:** 119–122. *pl. 34.* 1921.

yellowish-brown or hyaline under the microscope, 20–25 μ thick; basidia yellowish-brown or hyaline, 7–9 μ broad; spores yellowish-brown, smooth, elongate-ellipsoid, 7–9 x 5 μ; no cystidia or setae observed.

Habitat: ground-inhabiting, especially in burned-over regions, rare on coniferous wood.

Distribution: montane and subalpine zones. Widespread in the United States.

Occurrence: frequent. Throughout the season.

This ground-inhabiting fungus is most frequently found in regions where the trees have been destroyed by fires. The pilei often become confluent when the fruiting-bodies grow close together. Sticks, grass, and other forest-floor debris occasionally become imbedded in the fruiting-bodies. Infrequently, the pileus is covered with a cinereous pubescence which is in marked contrast to its usual dull-brownish color.

Polyporus perennis is related to *P. cinnamomeus*, both of which have similar hymenial characteristics. Sporophores of the former species are larger in size, and the surface of their pilei are of a dull brownish color, whereas the latter fungus is marked by its smaller size and its silky, shining, reddish-brown surface.

29. Polyporus cinnamomeus (Jacq.) Fries, Epicr. Myc. p. 429. 1838.

Boletus cinnamomeus Jacq. Coll. **1**: 116. 1786.

Strilia cinnamomea S. F. Gray, Nat. Arr. Brit. Pl. **1**: 645. 1821.

Polyporus parvulus Klotzsch, Linnaea **8**: 483. 1833. Not *P. parvulus* Schw. 1832.

Polyporus oblectans Berk. Lond. Jour. Bot. **4**: 51. 1845.

Polyporus splendens Peck, Ann. Rept. N. Y. State Mus. **26**: 68. 1874.

Polystictus cinnamomeus (Jacq.) Sacc. Michelia **1**: 362. 1878.

Polyporus subsericeus Peck, Ann. Rept. N. Y. State Mus. **33**: 37. 1880.

Coltricia cinnamomea (Jacq.) Murr. Bull. Torr. Bot. Club **31**: 343. 1904.

Plate 24, fig. 3.

Pilei gregarious, confluent, thin, circular, convex or umbilicate, 1–4 cm. in diameter, 1–3 mm. thick; surface zonate, radially adpressed-tomentose to -fibrillose, shining, Kaiser Brown; margin thin, acute, undulating to slightly lobed, sometimes fimbriate from the extension of the tomentum, occasionally sterile below; context less than 1 mm. thick, concolorous with the surface, hyphae of the context reddish-brown under the microscope, sometimes collapsed, branched, 6–8 μ in diameter; tubes adnate to slightly decurrent, 1–2 mm. long, Testaceous to Ferruginous; mouths angular, 2–3 per mm., concolorous with the tubes; stipe central, velvety, concolorous with the pileus, sometimes broadly attached, flat and branching, solid, often bulbous at the base, 1–4 cm. long, 1–3 mm. thick; dissepiments denticulate, 100–150 μ broad, tapered towards the mouths; trama concolorous with the context; hymenium loosely arranged, yellowish-brown to hyaline, 20–25 μ thick; basidia yellowish-brown to hyaline, 7–9 μ broad; spores yellowish-brown, smooth, elongate-ellipsoid, 7–9 x 5 μ; no cystidia or setae.

Habitat: on the ground in coniferous forests and aspen groves.

Distribution: montane and subalpine zones. Of frequent occurrence in the eastern United States; rare in the West.

Occurrence: rare. Autumn.

This small and delicate plant usually occurs in dense clusters with confluent pilei. The outstanding characteristics which separate it from *Polyporus perennis* are the reddish-brown color and the silky nature of the pileus.

Kauffman (*l. c.*) reports frequent collections of this fungus from Leal and Tolland, Colorado, during the month of September, 1917, and again in 1920. No other collections are known from Colorado.

30. Polyporus cryptopus Ellis & Barth. Erythea **4:** 79. 1896.
Scutiger cryptopus (Ellis & Barth.) Murr. Bull. Torr. Bot. Club **30:** 428. 1903.

Plate 25, fig. 3.

Pileus circular, convex, 3–4(7) cm. in diameter, 3–4 mm. thick; surface finely tomentose, smooth, white or gray, drying

wrinkled, Avellaneous; margin very thin, inflexed when dry, concolorous, entire; context white, drying Pinkish Buff, homogeneous, 1–2 mm. thick, hyphae of the context partially gelatinized, hyaline, branched, interwoven, 3–4 μ in diameter; tubes whitish, drying Warm Buff to Cinnamon-Buff, 1–2 mm. long, decurrent; mouths angular, large, 1–2 per mm., concolorous with the tubes; dissepiments thin, 80–150 μ, dentate; stipe central, bulbous at the base, solid, tomentose, 1.5–2 cm. long, 4–10 mm. thick, upper part concolorous with the tubes, lower part as dark as Snuff Brown, stipe almost entirely subterranean; hymenium 12–15 μ broad; basidia 6–8 μ in diameter; spores hyaline, smooth, ellipsoid, apiculate, 7–8 x 4 μ; no cystidia.

Habitat: ground, sometimes attached to grass roots.
Distribution: plains zone. Western and central United States.
Occurrence: rare. Spring and early summer.

The only record of the occurrence of this fungus in Colorado is a single collection made by Bethel, at Boulder, Colorado, in a field near the Chautauqua grounds. It is evidently found only in the plains and is characterized by its buried stipe and its round, whitish, coin-like cap.

b. Spores 12–16 x 4–6 μ.

31. Polyporus squamosus (Huds.) Fries, Syst. Myc. **1**: 343. 1821.

Boletus squamosus Huds. Fl. Angel. ed. 2. p. 626. 1778.
Polyporus caudicinus Murr. Jour. Myc. **9**: 89. 1903.

Plate 29, figs. 1–2.

Pileus fleshy when fresh, drying hard and very brittle, solitary in Colorado, reported usually as imbricate, sub-circular when young but soon becoming flabelliform, 10–40(50) cm. in diameter, 0.5–4 cm. thick; surface smooth, Pinkish Buff to Cinnamon Buff when fresh, drying Cinnamon-Buff to Clay Color, clothed with large appressed or free Snuff Brown to Sepia scales; margin thin, involute, slightly wavy; context soft and white when fresh, drying corky-friable, Light Buff or lighter, homogeneous, 0.5–3.5 cm. thick, hyphae of the context hyaline, branched, undulating,

4–8 μ in diameter; tubes decurrent as very shallow pits or reticulate ridges, at first the tubes are only reticulations, later, they develop up to 8 mm. long, white to Light Buff, drying Cinnamon; mouths large, angular and irregular, alveolar, 1–4 mm. broad, concolorous with the tubes; dissepiments round and broad at their free ends, about 600 μ thick, often pulled apart in dried plants; stipe lateral or excentric, variable as to size and shape, frequently rudimentary, at first obese, reticulate-poroid above and concolorous with the tubes, blackish below and often areolate, solid, homogeneous; hymenium compact, 20–30 μ thick; basidia 8 μ broad; spores hyaline, smooth, elongate-ovoid to -ellipsoid, apiculate, 12–16 x 5–6 μ; no cystidia.

Habitat: on deciduous hosts, especially cottonwoods (*Populus* spp.)

Distribution: known only from the plains zone in Colorado. Northeastern United States.

Occurrence: uncommon. Spring.

Type of rot: white rot.

Polyporus squamosus is generally found growing from the base of cottonwood (*Populus* spp.) stumps. It makes its appearance very early in the spring and develops to its maximum size by the early part of May. Although this fungus is rare in the United States, in Europe it is reported as being a common species that attacks frondose trees, especially the ash. This species is well marked by its large size, scaly pileus, and black stem.

32. **Polyporus hirtus** Quél. Champ. Jura et Vosges. **2**: 356. *pl. 2, f. 7.* 1873.

Polyporus hispidellus Peck, Ann. Rept. N. Y. State Mus. **52**: 649. 1899.

Scutiger hispidellus (Pk.) Murr. West. Polyp. p. 16. 1915.

Plate 27, fig. 3.

Pilei usually solitary, fleshy-tough, circular or sub-circular, convex or depressed, 5–14 cm. in diameter, 1–2.5 cm. thick; surface azonate, fibrillose, smooth, areolate or squamulose with age, Seal Brown to Bone Brown, not usually changing color on drying (Colorado specimens), or else fading to Wood Brown;

margin wavy-lobed, concolorous; context soft, homogeneous, white, drying hard, white to Light Buff, 3–20 mm. thick, hyphae of the context hyaline, thick-walled, undulating and irregular, branched, nodose-septate, 6–12 μ in diameter; tubes decurrent, 3–10 mm. long, white, drying Light Buff to Buckthorn Brown, occasionally blackish where bruised; mouths angular and irregular, 1–2 per mm., concolorous with the tubes; dissepiments thin, 80–120 μ thick, dentate; stipe lateral or excentric, often irregular, 2–5 cm. long, 1–5 cm. thick, solid, homogeneous, tomentose, white to Pinkish Buff; hymenium 24 μ broad; basidia large and conspicuous, 4-spored, 8–10 μ broad; spores elongate-ellipsoid, 12–16 x 4–6 μ when mature, hyaline, smooth; no cystidia.

Habitat: on rotted coniferous wood and on the ground.

Distribution: montane and subalpine zones. Found in the northern half of the United States.

Occurrence: rare. Late summer and autumn.

Polyporus hirtus, although a rare plant in the United States, has been collected in Colorado by both Overholts and Kauffman, and twice by the writer. The fresh plants are well marked by their dark brownish-gray, or brownish-purple pilei, and their whitish pores and stipes. In dried plants, the surface of the pileus rarely changes color, but the pores and stipe become a light yellowish-brown. The surface of the pileus becomes scaly after prolonged weathering, especially during the late autumn.

C. Spores cylindric.

a. Spores 8–10 x 3–4 μ.

33. Polyporus varius (Pers.) Fries, Syst Myc. **1**: 352. 1821.

Boletus varius Pers. Syn. Fung. p. 523. 1801.

Boletus calceolus Bull. Champ. p. 338. *pl. 360, 445.* 1791.

Polyporus calceolus (Bull.) Murr. Bull. Torr. Bot. Club **31**: 41. 1904.

Plate 27, figs. 4–7.

Pileus circular, reniform to flabelliform, sometimes with a depressed center, convex or nearly plane, 2–10 cm. in diameter, 3–10 mm. thick; surface radially striate, adpressedly-tomentose to almost glabrous, Clay Color to Ochraceous-Buff, radially

splotched with Hay's Russet; margin thin, obtuse, becoming wavy to lobed with age, concolorous to darker, Hay's Russet, Liver Brown to black, frequently sterile below; context white to Warm Buff, homogeneous, corky, 1–7 mm. thick, hyphae of the context yellowish under the microscope, branched, undulating, thick-walled, 4–5 μ in diameter; tubes 1–4 mm. long, decurrent, Cinnamon to Cinnamon Brown; mouths small, round to angular, 4–5 per mm., concolorous with the tubes; stipe excentric or lateral, rarely central, woody, solid, 1–4 cm. long, 4–10 mm. thick, tomentose to glabrous, upper portion concolorous with the hymenium, lower portion abruptly black and laccate; dissepiments golden under the microscope, at first as thick as 300 μ, later thinner, 50–100 μ; hymenium hyaline, compact, present in young plants, apparently absent in older ones, 16–20 μ thick; basidia 7–8 μ in diameter; spores hyaline, smooth, cylindric, 8–10 (12) x 3–4 μ.

Habitat: on various deciduous hosts, especially *Populus tremuloides.*

Distribution: montane zone. Widespread in the United States.

Occurrence: common some years, rare or absent during others. Summer and autumn.

Type of rot: white rot.

Polyporus varius, *P. elegans*, and *P. picipes* represent three closely related species which vary from one another mainly in the size of their fructifications and the color of their pilei. So far as the writer is informed, *P. picipes* has never been collected in Colorado and it may not occur there. The surface of the pileus of *P. varius* is marked with radially striate, reddish-brown bands, whereas that of *P. elegans* is always tan-colored with none of the above markings.

34. **Polyporus elegans** (Bull.) Fries, Epicr. Myc. p. 440. 1838.
Boletus elegans Bull. Herb. Fr. *pl. 46.* 1780.
Boletus nummularis Bull. *ibid. pl. 124.* 1782.

Plate 27, figs. 1–2.

Pileus circular, reniform to flabelliform, sometimes with a depressed center, convex or nearly plane, 1–7 cm. in diameter, 2–8

mm. thick; surface azonate, occasionally very faintly radially striate but never markedly so, pruinose to glabrous, Light Ochraceous-Buff to Cinnamon, rarely fading out to white; margin thin, becoming wavy or much lobed with age, concolorous or darker as: Bay to Chestnut, in young plants frequently sterile below; context white to Warm Buff, homogeneous, corky, 1–5 mm. thick, hyphae of the context yellowish under the microscope, branched, undulating, thick-walled, 4–5 μ in diameter; tubes 1–3 mm. long, decurrent, Cinnamon to Cinnamon-Brown; mouths small, round to slightly angular, 4–5 per mm., concolorous with the tubes; stipe excentric or lateral, rarely central, woody, solid, 1–4 cm. long, 2–6 mm. thick, pruinose to glabrous, upper portion concolorous with the hymenium, lower portion abruptly black and laccate, scutate or rooting at the base; dissepiments golden under the microscope, at first as thick as 300 μ, later thinner, 50–100 μ; hymenium hyaline, compact, present in young specimens, apparently absent in old ones, 16–20 μ thick; basidia 7–8 μ in diameter; spores hyaline, smooth, cylindric, 8–10(12) x 3–4 μ.

Habitat: various deciduous hosts, especially *Populus tremuloides.*

Distribution: montane zone. Widespread in the United States.

Occurrence: common some years, rare or absent during others. Summer and autumn.

Type of rot: white rot.

Polyporus elegans is closely related to *P. varius* and some care must be exercised in separating them (see p. 359). This fungus evidently persists for several years, during which time it remains attached to its substratum. Under long exposure to the elements, it often becomes bleached to a dirty white, and the tubes are very much disorganized and cracked as shown in plate 27, fig. 1.

b. Spores 5–6 x 1.5–2.5 μ.

35. **Polyporus osseus** Kalchb. Math. Term. Közlem. **3:** 217. *pl. 1, f. 2.* 1865; Hedwigia **4:** 141. 1865.

Polyporus Zelleri Murr. West. Polyp. p. 13. 1915.

Plate 29, fig. 3.

Pilei imbricate or caespitose-multiplex, cohesive to confluent,

fleshy-tough, drying rigid to horny, flabelliform or conchate, 2–8 x 2–10 x 0.5–0.9 cm.; surface tomentose to nearly glabrous, at first white, light gray to light yellowish-brown, drying wrinkled and Drab-Gray, Light Pinkish Cinnamon to Sayal Brown; margin thin, entire, undulating, occasionally lobed, concolorous or white, inflexed on drying; context fleshy, white, drying horny, Pale Ochraceous-Salmon, 3–8 mm. thick, usually with a paper-thin brown line adjacent to the tubes, hyphae of the context hyaline, septate and nodose-septate, thin-walled, undulating, profusely branched, of varying thicknesses, (6)8–12 μ in diameter; tubes decurrent, white to yellowish, drying Warm Buff to Ochraceous-Tawny, 1–3 mm. long; mouths angular, 4–6 per mm., concolorous with the tubes; dissepiments thin, 80–120 μ broad, becoming lacerate at the mouths; stipe lateral or excentric, confluent, occasionally branched, 4–12 mm. thick, 1–3 cm. long, color and substance similar to that of the pileus; hymenium hyaline, 8–12 μ thick; basidia hyaline, small, 8–9 x 3–4 μ; spores hyaline, smooth, cylindric, occasionally curved, 5–6 x 1.5–2.5 μ; no cystidia observed.

Habitat: attached to exposed dead roots of living *Picea Engelmanni;* on rotten coniferous wood, or on the ground in coniferous forests.

Distribution: montane zone. Scattered throughout northern United States.

Occurrence: rare. Summer and autumn.

Type of rot: unknown.

This is a rare plant in both America and Europe. As pointed out by Lloyd,[52] the European specimens are white when fresh and when dry, whereas the American ones are gray to yellowish-brown in color. *Polyporus Zelleri* is only a drab form of this species and represents the species as it is usually found in America.

Only a single collection of this plant is known from Colorado. This was collected by Kauffman at Leal, Colorado, in 1917, and reported as, ". . . at base of living trunk of Picea Engelmanni on the exposed dead part of a root."[53]

The particular growth-form illustrated in plate 29 is character-

[52] Lloyd, C. G. Synopsis of the stipitate Polyporoids. p. 191. 1912.
[53] Kauffman, C. H. *l. c.* p. 122.

istic of this plant. Furthermore, in mature specimens a very thin dark line is found adjacent to the tubes, but this is absent in young and immature ones.

TRAMETES

Trametes Fries, Gen. Hymen. p. 10. 1836.

Plants annual or perennial, lignicolous, coriaceous to corky, sessile, effused-reflexed, or resupinate; context varying in thickness and color, usually continuous with and of the same texture as the trama; tubes forming one or occasionally several layers, usually joined to the context in an uneven line so that they appear to be sunk into the context to unequal depths; pore-mouths circular, angular to daedaloid, usually of a large diameter; spores smooth, hyaline, elongate-ellipsoid to cylindric, occasionally curved; cystidia absent, setae and hyphal pegs present or absent.

This genus is not well differentiated from *Polyporus* on one hand, and from *Fomes*, on the other. The Friesian characterization, based on the continuity of the hyphae of the trama and context, has proved to be inadequate.[54] Indeed, it probably would be better to disregard this genus and place the so-classified plants in the genus *Polyporus* or *Fomes*, depending on their structure. Since, however, the genus *Trametes* is accepted by recent European and American writers, it would be unwise to disregard it here. Irrespective of the similarity between this and other genera, no difficulty should be experienced in identifying these plants, for all species of the genus *Trametes* are separated in the keys to the species of *Polyporus* and *Fomes*, as well as in the key to the species of *Trametes*.

KEY TO THE SPECIES[55]

Context white or whitish; setae and cystidia absent........................1
Context light brown to wood-color; setae and cystidia absent................5
Context darker, dark brown to dark rusty-brown; setae present; cystidia none..6
Context rose-colored, pinkish or flesh-colored..............................9

1. Pileus more than 1 cm. thick..............................*41. T. hispida*
Pileus less than 1 cm. thick..2

2. Pileus brown, or with a conspicuous brown pubescence........................3
Pileus white to whitish; pores 1–3 mm. broad; usually on coniferous hosts. ....*39. T. heteromorpha*

---

[54] Ames, A. Ann. Myc. 9: 211–253. 1913.

[55] See footnote, p. 318.

3. Mouths of the tubes averaging 2–3 or more per mm.; usually on conifers. .... *37. T. serialis*
   Mouths of the tubes averaging 1–2 per mm. 4
4. Pileus less than 3 mm. thick; hymenium poroid, daedaloid to lamellate; on conifers. .... *38. T. variiformis*
   Pileus more than 3 mm. thick; on deciduous hosts. .... *41. T. hispida*
5. Context homogeneous, not containing a black line; pileus hirsute to hispid, yellowish-brown to brown. .... *41. T. hispida*
   Context duplex, containing a thin black line; pileus finely tomentose to glabrous, umber-brown to blackish. .... *40. T. stereoides*
6. Setae present in the hymenium. 8
   Setae absent. 7
7. Tubes whitish within; dissepiments rather thin; on conifers. .... *42. T. odorata*
   Tubes not whitish within; dissepiments thin. .... *56. Lenzites trabea*
8. Spores globose to subglobose; margin of the pileus lighter-colored than the rest of the pileus; pileus dark brown, zonate; mouths ochraceous-orange to brown. .... *46. Fomes Pini*
   Spores cylindric; surface and margin of the pileus concolorous, zonate; mouths reddish-brown, slightly darker than the above. .... *36. T. isabellina*
9. Sporophores ungulate. .... *52. Fomes roseus*
   Sporophores dimidiate to conchate. .... *43. T. subrosea*

1. Setae present and abundant.

36. Trametes isabellina Fries, Hymen. Eur. p. 585. 1874.

Fomes tenuis Karst. Medd. Soc. Fauna. Fl. Fenn. **14**: 81. 1887.

Polyporus tenuis (Karst.) Romell, Arkiv f. Bot. **11**^{3}: 24. 1911. Not *Polystictus tenuis* Sacc. 1888.

Trametes setosus Weir, Jour. Agr. Res. **2**: 164. 1914.

Phellinus isabellinus (Fr.) Bourd. & Galz. Hymen. Fr. **1**: 622. 1927.

Trametes tenuis (Karst.) of most American authors.

Plate 30, figs. 1–2.

Sporophores annual or perennial, woody, conchate, sessile or effused-reflexed, imbricate, confluent, 0.5–2.5 x 1–15 x 0.2–1 cm., or entirely resupinate, 1–10 x 3–50 cm. or more; surface hirsute, zonate, Argus Brown, Mars Brown, Prout's Brown to almost black; margin even to undulating, at first rounded, velvety-tomentose, sterile, Antique Brown, with age becoming acute, fertile, and concolorous with the surface; context homogeneous, 1 mm. or less in thickness, Argus Brown to Brussels Brown,

hyphae of the context reddish-brown under the microscope, straight, apparently unbranched and aseptate, thin-walled, 2.5–3 μ in diameter; tubes rarely stratified, in effused-reflexed specimens often oblique, 1–10 mm. long each season, Sudan Brown to Brussels Brown, fulvous within; mouths concolorous with the tubes, round to angular, 3–5 per mm.; free ends of the dissepiments thick, tomentose, 50–100 μ thick; hymenium hyaline, incrusted, incrustation soluble in KOH solution, 8–10 μ broad; basidia hyaline, 3–4 μ broad; spores hyaline, smooth, cylindric, 6–9 x 2 μ; setae abundant, pointed, 7–9 μ broad at their bases, projecting up to 50 μ.

Habitat: on coniferous hosts, especially *Picea Engelmanni.*

Distribution: montane and subalpine zones. Widespread in the United States.

Occurrence: common. Summer and autumn.

Type of rot: white rot.

Due to the fact that this fungus is frequently found in a *Poria*-like growth-form, it would follow that it may have been described as a *Poria*. Overholts[56] is of the opinion that *Poria viticola* (*Fuscoporia viticola*), *P. contigua*, and *P. superficialis* are all closely related to *T. isabellina* and probably conspecific. Most of these *Porias*, however, have larger and more daedaloid pores than those described for *T. isabellina;* but as conceded by Overholts (*l. c.*), intermediate stages between these various conditions may be found. An adequate disposition of the *Porias* mentioned above can not at present be given by the writer, yet it seems advantageous to point out the fact that they are probably conspecific. These *Porias* are found on a wide range of deciduous hosts.

The reflexed portion of this fungus is never thick or *Fomes*-like, and it is scarcely probable that it could be confused with *Fomes Pini.* It does, however, have a close resemblance to *Fomes nigrolimitatus*, which differs chiefly in having a black line in the context. Compare *Poria ferruginosa* with resupinate specimens of this species.

2. Neither setae nor cystidia present in the hymenium.

A. Spores elongate-ellipsoid, large, 8 μ or more in length.

[56] Overholts, L. O. Mycologia **15:** 227–229. 1923; *ibid.* **23:** 127–128. 1931.

37. **Trametes serialis** Fries, Hymen. Eur. p. 585. 1874.
Polyporus serialis Fries, Syst. Myc. **1**: 370. 1821.
Polyporus callosus Fries, *ibid.* 381.
Polyporus scalaris Pers. Myc. Eur. **2**: 90. 1825.
Poria callosa (Fr.) Sacc. Syll. Fung. **6**: 298. 1888.
Coriolellus serialis (Fr.) Murr. N. Am. Fl. **9**: 29. 1907.

Plate 30, fig. 3.

Pileus coriaceous, effused-reflexed, occasionally resupinate, laterally confluent, narrowly reflexed, 0–2 x 1–15 x 0.3–1 cm.; surface appressed-tomentose, zonate, Warm Buff to Buckthorn Brown; margin thin, acute, undulating to lobed, concolorous; context thin, less than 1 mm., white, hyphae hyaline, branched, containing very few septa, incrusted, 2–4 μ in diameter; tubes white, 2–8 mm. long; mouths white to Light Buff, variable in size and shape, circular to angular, 2–3 per mm.; free edges of the dissepiments at first thick and entire, with age becoming thin and dentate, 120–250 μ thick; hymenium hyaline, rarely containing globose tuberculose masses of crystalline matter up to 15 μ in diameter, 15–22 μ thick; basidia hyaline, 5–6 μ broad; spores smooth, hyaline, cylindric-ellipsoid, 7–9 x 2–3(4) μ; no cystidia.

Habitat: on various coniferous and deciduous hosts.

Distribution: foothill, montane, and subalpine zones. Widespread in the United States.

Occurrence: uncommon. Summer and autumn.

Type of rot: brown rot.

The general growth-form of this fungus is effused-reflexed and similar to that of *T. variiformis* and *T. heteromorpha.* The latter two species, however, have large pores averaging 1 mm. or more in diameter, whereas *T. serialis* has very much smaller pores, averaging 2–3 per mm.

Poria callosa is the resupinate form of this species.

38. **Trametes variiformis** Peck, N. Y. State Mus. Bull. **28**: 220. 1899.
Polyporus variiformis Peck, Ann. Rept. N. Y. State Mus. **42**: 26. 1889.
Coriolellus serialis (Fr.) Murr. N. Am. Fl. **9**: 29. 1907. In part.

Plate 30, fig. 4.

Sporophores coriaceous, effused-reflexed, laterally connate, often entirely resupinate, 0.2–2 x 2–25 x 0.2–1 cm.; surface hirsute, zonate, Mummy Brown, Bone Brown to blackish; margin undulating, obtuse, hirsute, Mummy Brown, fertile below; context less than 1 mm. thick, duplex, upper layer concolorous with the surface, lower layer white, hyphae sparingly branched, incrusted, 4–6 μ in diameter; tubes 1–10 mm. long, usually obliquely arranged and opened laterally, Light Pinkish Cinnamon to Cinnamon-Buff; mouths concolorous, angular, daedaloid to labyrinthiform, averaging 1–2 per mm.; dissepiments with age becoming lacerate, thick, 200–600 μ; hymenium hyaline, compact, 20–30 μ broad; basidia hyaline, 7–9 μ broad; spores hyaline, smooth, elongate-ellipsoid, 8–12 x 4–5 μ; no cystidia.

Habitat: known only from coniferous hosts.

Distribution: montane and subalpine zones. Northern part of the United States.

Occurrence: common. Autumn.

Type of rot: white rot.

This fungus is frequently found in a resupinate growth-form, and then it may be confused with *T. heteromorpha* (see page 367). The effused sporophores, with their narrowly reflexed dark-colored margin and the obliquely arranged tubes, are characteristic.

39. Trametes heteromorpha (Fr.) Lloyd, Mycol. Notes **5**: 848. *f. 1416–1419.* 1919.

Daedalea heteromorpha Fries, Obs. Myc. **1**: 108. 1815.
Lenzites heteromorpha Fries, Epicr. Myc. p. 407. 1838.
Coriolellus Sepium (Berk.) Murr. Bull. Torr. Bot. Club **32**: 481. 1905. In part.
Coriolus hexagoniformis Murr. N. Am. Fl. **9**: 20. 1907.
Trametes laceratus Lloyd, Mycol. Notes **4**: 604. 1916.

Plate 31, fig. 2.

Sporophores coriaceous, effused-reflexed and laterally connate, often resupinate, 0.2–3 x 2–30 x 0.1–1 cm.; surface tomentose, zonate, white, Light Buff to Pinkish Buff; margin obtuse, undulating to lobed, tomentose, concolorous, fertile below; context 1

mm. or less thick, homogeneous, white to Light Buff, hyphae of the context hyaline, branched, incrusted, 3–5 μ in diameter; tubes 0.2–3 cm. long, often obliquely arranged and then opened laterally, Light Buff to Cinnamon-Buff; mouths angular, daedaloid to labyrinthiform, 1–3 mm. broad, concolorous with the tubes; dissepiments lacerate, rather thick, 250–300 μ; hymenium hyaline, compact, 20–40 μ broad; basidia hyaline, 6–8 μ broad; spores smooth, hyaline, elongate-ellipsoid, apiculate, 8–12 x 3–4 μ; no cystidia.

Habitat: mainly on conifers, especially *Picea Engelmanni.*

Distribution: montane and subalpine zones. Widespread through the northern part of the United States.

Occurrence: rare. Autumn.

Type of rot: brown rot.

Only a single collection of this fungus is known from Colorado. This was made on Pikes Peak by I. M. Johnston and sent to Lloyd for determination.

Trametes heteromorpha is characterized at once by its large pores and white or yellowish-white pileus. The closely related *T. variiformis*, in addition to having smaller pores than this species, has a dark-colored pileus. If, however, these species are found entirely resupinate, their identification rests entirely upon the size of the pores, for the spores and other hymenial characters are similar.

40. Trametes stereoides (Fr.) Bres. Hymen. Kmet. in Atti Accad. Roveret. III. **3**: 92. 1897.

Polyporus stereoides Fries, Obs. Myc. **2**: 259. 1818; Syst. Myc. **1**: 369. 1821.

Polyporus cervinus Pers. Myc. Eur. **2**: 87. 1825.

Daedalea mollis Sommerf. Suppl. Fl. Lapp. p. 271. 1826.

Trametes mollis (Sommerf.) Fries, Hym. Eur. p. 585. 1874.

Antrodia mollis (Sommerf.) Karst. Medd. Soc. Fauna Fl. Fenn. **5**: 40. 1879.

Plate 31, fig. 1.

Sporophores coriaceous, effused-reflexed or entirely resupinate, separable, reflexed portion imbricate, conchate, 0.5–4 x 1–10 x 0.2

–0.5 cm.; surface tomentose, zonate, uneven, Tawny-Olive, Bone Brown to almost black; margin thin, concolorous, at length revolute; context rarely over 1 mm. thick, duplex, Clay-Color next to the tubes, Tawny-Olive to Bone Brown above, separated by a paper-thin, black line, hyphae adjacent to the tubes hyaline under the microscope, much branched, 1–3 μ in diameter; tubes 1–4 mm. long, occasionally stuffed, avellaneous within; mouths variable in shape and size, circular to sinuous, averaging about 1 per mm., Cinnamon-Buff to Clay Color; dissepiments frequently torn, of varying thicknesses, 200–600 μ; hymenium hyaline, 18–22 μ broad; basidia hyaline, 5–7 μ in diameter; spores hyaline, smooth, cylindric, apiculate, occasionally curved, 9–12 x 3.5–4.5 μ; no cystidia.

Habitat: mainly on deciduous hosts, rare on conifers.

Distribution: montane and subalpine zones. Northern half of the United States.

Occurrence: rare. Autumn.

Type of rot: unknown.

This fungus is well marked by its large pores and brownish-colored duplex context. The black line between the layers of context is an important character, but should be correlated with other characters in order to avoid confusion with *Fomes nigrolimitatus*, *F. conchatus*, *Polyporus ovinus*, and *P. osseus*, which also have a similar black line in the context.

41. Trametes hispida Pass. Nuov. Giorn. Bot. Ital. **4:** 155. 1872.

Polyporus Lindheimeri Berk. & Curt. Grevillea **1:** 50. 1872.
Irpex grossus Kalchbr. *ibid.* **10:** 57. 1881.
Trametes Peckii Kalchbr. Bot. Gaz. **6:** 274. 1881.
Polystictus scuirinus Kalchbr. in Thüm. Pilz Fl. Sib. V. **14:** 897. 1882.
Polystictus Fergussoni Cooke, Grevillea **15:** 23. 1886.
Polystictus Celottianus Sacc. & Manc. in Sacc. Syll. Fung. **6:** 249. 1888.
Funalia stuppea (Berk.) Murr. Bull. Torr. Bot. Club **32:** 356. 1905.

Plate 31, fig. 3.

Pileus annual or perennial, corky, dimidiate, sessile or effused-reflexed, rarely subresupinate, imbricate, 2–10 x 2–25 x 0.5–5 cm.; surface clothed with long, stiff, erect, rarely adpressed hairs, 1–4 mm. in length, Sanford's Brown to Bay, fading with age to Cinnamon-Buff, azonate or occasionally indistinctly zonate; margin acute or rounded, entire or slightly undulate, concolorous, clothed with stiff hairs or else finely hirsute; in vertical section the hairy layer is 1–10 mm. thick, zonate in old and perennial specimens; context corky-hard, azonate, Clay Color, 0.2–2 cm. thick, hyphae of the context branched, septate, of two kinds: brown-colored, sparingly branched, 5–8 μ in diameter, and hyaline or yellowish-colored, profusely branched, 2–4 μ in diameter; tubes in annual specimens 2–10 mm. long, white within, in perennial forms the tubes are continuous up to 3 cm., older regions white-stuffed; trama of the tubes concolorous with the context; mouths angular to irregular, averaging about 1 per mm., Buckthorn Brown; dissepiments 90–300 μ thick; hymenium hyaline, 18–22 μ broad; basidia hyaline, 8–10 μ broad, projecting up to 12 μ; sterigmata 4–6 μ long; spores hyaline, smooth, cylindric, 12–14 x 4 μ; no cystidia observed.

Habitat: on various deciduous hosts, especially members of the Salicaceae.

Distribution: plains and foothill zones. Widespread in the United States.

Occurrence: common. Spring and summer.

Type of rot: white rot.

Smith[57] has recently reported that this fungus is a wound parasite of apple trees. The writer has found it to be a wound parasite of cottonwood (*Populus* spp.) trees on the campus of the University of Colorado.

The long brownish hairs on the pileus and the large basidia and spores distinctly mark this species.

The validity of the specific name used above for this fungus has been attacked by various writers. *Trametes gallica*, which has prior rank, is considered by Lloyd[58] as probably a thin form of *T. hispida*, but markedly different from the latter species as it

[57] Smith, E. C. Mycologia **22**: 221–222. 1930.

[58] Lloyd, C. G. Mycol. Notes **4**: 520. *f. 517.* 1912.

is known in America. He furthermore states that most of the European mycologists consider the former species to be valid and distinct. Bourdot and Galzin[59] place *T. gallica* in their "Espèces non observées, d'interprétation douteuse, ou de classification incertaine," whereas Bresadola[60] considers it to be conspecific with *T. hispida*. Murrill[61] considers *Trametes stuppeus*, which likewise has prior rank, to be synonymous with *T. hispida* (*T. Peckii*). Since in the recent work of Bourdot and Galzin (*l. c.*), *Trametes hispida* is considered to be the valid name, and since these workers had access to the types of both *Trametes gallica* and *T. stuppeus*, their precedence will be followed in this treatise. In so doing, the writer feels that there is an advantage in retaining the well-known name that more than compensates for juggling the species among doubtful prior names.

Many of the older mycological workers knew this plant under the name of *Trametes Peckii*, which is now generally conceded to be synonymous with *T. hispida*. Since the latter name is the older one, it should be used.

42. **Trametes odorata** (Wulf.) Fries, Epicr. Myc. p. 489. 1838.
Boletus odoratus Wulf. in Jacq. Collect. ad. Bot. **2**: 150. 1788.
Polyporus odoratus (Wulf.) Fries, Syst. Myc. **1**: 373. 1821.
Lenzites saepiaria porosa Peck in Port. & Coult. Fl. Colo., U. S. Dept. Int. Geol. & Geog. Surv. Misc. Publ. 4: 164. 1874.
Ochroporus odoratus (Wulf.) Schroet. Krypt. Fl. Schles. p. 488. 1889.
Gloeophyllum hirsutum (Schaeff.) Murr. Jour. Myc. **9**: 94. 1903. In part.
Trametes protracta Fr. of most American authors.

Plate 31, fig. 4.

Pileus annual or perennial, sessile, somewhat coriaceous, pulvinate to dimidiate, occasionally ungulate, 1–5 x 2–12 x 0.5–2 cm.; surface zonate, at first strigose-hirsute, Antique Brown to Russet, with age becoming adpressedly strigose to glabrous, Raw Umber, Mummy Brown to blackish, or with age bleaching

[59] Bourdot, H., & A. Galzin. Hymen. Fr. **1**: 692. 1927.
[60] Bresadola in Sacc. Syll. Fung. **23**: 378, 442, 479. 1925.
[61] Murrill, W. A. *l. c.*

to Avellaneous, Light Drab to Smoke Gray; margin rounded to obtuse, hirsute, concolorous or lighter, sterile below; context firm, homogeneous to indistinctly zonate, Argus Brown, occasionally lighter-colored near the surface, 0.5–3 cm. thick, hyphae of the context brown under the microscope, apparently unbranched, with few septa, rather thin-walled, 3–6 μ in diameter; tubes 0.3–1 cm. long, concolorous, fulvous within; mouths angular, daedaloid to labyrinthiform, irregular in size and shape, averaging 1–2 per mm., Cinnamon-Buff to Prout's Brown, walls thick and tomentose, with age becoming thin and glabrous; dissepiments of varying thicknesses, 200–800 μ; hymenium hyaline, compact, 35–40 μ thick; basidia hyaline, 5–7 μ broad, 4-spored; spores hyaline, smooth, cylindric to elongate-ellipsoid, apiculate, rarely curved, 8–12 x 3–5 μ; no cystidia observed.

Habitat: decorticated and charred coniferous wood. No deciduous hosts are known.

Distribution: from the foothill zone up to the subalpine zone. Widespread in the United States.

Occurrence: common. Spring, summer, and autumn.

Type of rot: brown rot.

In America, *Trametes odorata* has generally been known under the name of *T. protracta*, due to misinterpretations by earlier workers. In fact, the latter species appears to be very close to *Lenzites trabea* and probably is conspecific with it.

Murrill (*l. c.*) evidently was of the opinion that *T. odorata* was the poroid form of *Lenzites saepiaria*. The writer, however, has found the latter plant to be lamellate from the very earliest stage, whereas *T. odorata* may be labyrinthiform, but never truly lamellate. Snell *et al.*[62] have contributed rather conclusive evidence which supports the separation of these species.

This fungus is most always narrowly extended and of considerable length, and never *Fomes*-like in structure. The surface of the fruiting bodies usually bleaches with age to a grayish-color; more rarely, and in extremely damp locations, it becomes blackish.

B. Spores cylindric to allantoid, 6–8 x 2–3 μ.

[62] Snell, W. H., W. G. Hutchinson, and K. H. N. Newton. Mycologia **20**: 276–291. 1928.

43. Trametes subrosea Weir, Rhodora **25**: 217. 1923.
Trametes carnea Cooke. In the American sense only.

Plate 32, fig. 1.

Pileus annual or perennial, sessile or effused-reflexed, dimidiate, often imbricate and longitudinally effused for a distance of 50 cm. or more, 2–6 x 2–15 x 0.5–2 cm.; surface zonate, at first velvety-tomentose, Salmon-Buff to Buff Pink, with age becoming radially adpressed-fibrillose or nearly glabrous, Fuscous, Dark Brown to black; margin acute, concolorous, or lighter, as Salmon-Buff to Buff Pink, sterile below; context 2–10 mm. thick, firm-corky, indistinctly multizonate, Japan Rose to Congo Pink, hyphae yellowish-brown under the microscope, sparingly branched, thick-walled, apparently aseptate, 3–5 μ in diameter; tubes concolorous with the context, indistinctly stratified, white-stuffed in the older layers, white-lined in the younger ones, 1–4 mm. long each season; mouths concolorous, round to slightly angular, 3–5 per mm.; dissepiments 60–140 μ broad, yellowish-brown; hymenium hyaline, 15–20 μ broad; basidia hyaline, 5–6 μ broad, projecting up to 8 μ, sterigmata up to 4 μ long; spores smooth, hyaline, cylindric, sometimes allantoid, 6–8 (9) x 2–3 μ; no cystidia observed.

Habitat: on various coniferous hosts, rare on deciduous ones.

Distribution: from the foothills up to the subalpine zone. Widespread in the United States.

Occurrence: common. Throughout the year.

Type of rot: brown rot.

As pointed out by Weir,[63] the American plant which he named *Trametes subrosea* differs fron *T. carnea* in that the surface of the former is zonate and velvety-tomentose, whereas that of the latter is glabrous and azonate. Up to comparatively recent times, this American plant has been called *T. carnea*.

Murrill[64, 65] combines *Trametes subrosea* (*T. carnea*) with *Fomes roseus*, and considers the former species to be only a growth-form of the latter. Weir (*l. c.*), however, points out distinct morpho-

[63] Weir, J. R. *l. c.*
[64] Murrill, W. A. North American Flora 9: 95. 1907.
[65] ————, Mycologia 12: 13. 1920.

logical differences; and recently, Snell *et al.*[66] further confirm the separation of these two species by presenting physiological differences. *Trametes subrosea* is always dimidiate and the context is dark rose-colored, whereas *Fomes roseus* is always ungulate and the context is light rose-colored.

Although this fungus is most frequently found on coniferous hosts, Zeller[67] has recently reported it to be a wound parasite on peach and plum trees.

GANODERMA

Ganoderma Karst. emend. Pat. Hymen. Eur. p. 142. 1887; Karsten, Rev. Myc. 3[9]: 17. 1881.

Pileus annual to perennial, sessile to stipitate; surface either laccate and shining or incrusted and dull; crust thick, rigid, brittle, formed of thickened hyphal elements; context light- to dark-brown; pores white to brown; spores truncate at their apexes when mature, yellow to brown under the microscope, epispore hyaline and smooth, endospore colored when mature and having wart- or spine-like processes extending into the epispore; setae and cystidia absent.

The outstanding characteristic of this genus is the colored, truncate spores, which usually have the appearance, under the oil-immersion lens, of being spined, verrucose, or punctate; but as explained by Coleman,[68] the outer spore wall is always smooth and hyaline, whereas the inner wall is colored and more or less spined. In addition to these spore characteristics, there also are external ones which are discernible to the unaided eye, as: laccate or heavily incrusted pileus and stipe (if present) and brown context.

The genus as defined above is in the sense of Karsten emended by Patouillard in 1887. Haddow[69] has recently reviewed the history of the genus and includes a critical study of several of the more common species. He follows Karsten's conception, which limits the genus to those species with varnished pilei and with the

[66] Snell, W. H., W. G. Hutchinson, and K. H. N. Newton. Mycologia **20**: 276–291. 1928.

[67] Zeller, S. M. Jour. Agr. Res. **33**: 687–693. 1926.

[68] Coleman, L. C. Bot. Gaz. **83**: 48–60. 1927.

[69] Haddow, W. R. Jour. Arnold Arbor. **12**: 25–46. 1931.

characteristic spore structure as previously defined. *Ganoderma applanatum* is not included because it lacks the varnished pileus. On the other hand, the writer wishes to emphasize the emendation by Patouillard who, not without reason, emphasized the spore structure rather than the varnished pileus. It is thought that by adopting this emendation less varying generic limitations are established.

44. **Ganoderma applanatum** (Pers.) Pat. Bull. Soc. Myc. Fr. **5:** 67. 1889.

Boletus lipsiensis Batsch, Elench. Fung. p. 183. *pl. 25, f. 130a, b.* 1786.

Boletus applanatus Pers. Obs. Myc. **2:** 2. 1799.

Polyporus applanatus (Pers.) Wallr. Fl. Crypt. Germ. **4:** 591. 1833.

Polyporus megaloma Lév. Ann. Sci. Nat. Bot. III. **5:** 128. 1846.

Polyporus leucophaeus Mont. Syll. Crypt. p. 157. 1856.

Fomes applanatus (Pers.) Gill. Champ. Fr. **1:** 686. 1878.

Fomes leucophaeus (Mont.) Cooke, Grevillea **14:** 18. 1885.

Fomes megaloma (Lév.) Cooke, *ibid.*

Placodes applanatus (Pers.) Quél. Fl. Myc. Fr. p. 400. 1888.

Elfvingia applanata (Pers.) Karst. Finl. Basidsv. p. 334. 1889.

Phaeoporus applanatus (Pers.) Schroet. Krypt. Fl. Schles., Pilze, 1 Hälfte, p. 490. 1889.

Ganoderma leucophaeum (Mont.) Pat. Bull. Soc. Myc. Fr. **5:** 73. 1889.

Elfvingia lipsiensis (Batsch) Murr. Bull. Torr. Bot. Club **30:** 297. 1903.

Elfvingia megaloma (Lév.) Murr. *ibid.* 300.

Ganoderma lipsiensis (Batsch) Atk. Ann. Myc. **6:** 189. 1908.

Plate 32, fig. 4.

Sporophores perennial, sessile, applanate, rarely ungulate, 5–30 x 5–50 x 1–15 cm.; surface plane or convex, concentrically furrowed, incrusted, crust broken due to the soft underlying context, pulverulent, never shining except where rubbed, variously

colored, as: Light Buff, Drab-Gray, Hair Brown, Cinnamon, Walnut Brown to blackish; margin round, sterile below, white to Light Buff; crust 1 mm. or less in thickness, horny, blackish or dark brown and shining in section, made up of irregularly arranged, swollen hyphal ends; context soft, zonate, 2–12 mm. thick, variously colored, as: Light Buff, Hazel to Carob Brown; hyphae of the context sparingly branched, undulating, thick-walled, brown, 4–7 μ in diameter; tubes evenly stratified, separated by a thin layer of context, 0.5–2 mm. thick, 3–18 mm. long each season, older ones usually white-stuffed, young ones approximately concolorous with the context; mouths circular, 4–6 per mm., when young white, Cartridge Buff to Massicot Yellow, turning darker where bruised, with age becoming concolorous with the tubes; dissepiments thin, 40–80 μ broad; hymenium hyaline to yellowish under the microscope, 16–25 μ thick, containing simple or forked, unequally thickened hyphae which extend beyond the basidia and which do not have the characteristics of cystidia; basidia hyaline to yellowish, 5–7 μ broad; spores brown, appearing to be minutely spined, ovoid, truncate, 8–9 x 5–6 μ.

Habitat: deciduous hosts, especially species of *Populus* and *Betula;* rare on conifers.

Distribution: montane zone. Widespread in the United States.

Occurrence: frequent. Throughout the year.

Type of rot: white rot.

The spores found on the upper surface of the pileus are basidiospores that were carried there by convection currents of air. They were previously considered to be conidia until White[70] definitely disproved this assumption. The spore structure, the brown context, and the horny crust distinctly characterize this species.

Although this species does not have a varnished crust, which to some extent characterizes this genus, its cellular structure is nevertheless essentially the same as that of the crust of varnished members. The crust is composed of swollen hyphal ends irregularly arranged, whereas in the species with a varnished crust the swollen hyphal ends are arranged in a palisade-like layer.

[70] White, J. H. Trans. Roy. Can. Inst. 12: 133–174. 1920.

The spores of *G. applanatum* are similar in structure to those found in species having a varnished crust. These characteristics seem to warrant the inclusion of this species in the genus *Ganoderma* as emended by Patouillard, and as included by him.

Both the light- (*Fomes leucophaeus*) and dark-colored forms are found in Colorado; the former form, however, is more frequently encountered.

This fungus is both parasitic and saprophytic on a wide range of deciduous and coniferous hosts (White, *l. c.*), but in Colorado it occurs most frequently on dead *Populus tremuloides.*

FOMES

Fomes (Fr.) Gill. Champ. Fr. **1**: 682. 1878; Fries, Nov. Symb. p. 31. 1851.

Plants always at length perennial, lignicolous, corky to woody, usually large and massive, ungulate to applanate, sessile, occasionally effused-reflexed; surface incrusted or anoderm; context of varying thicknesses and colors; tubes at length stratified, strata may or may not be separated by a layer of context; pore-mouths circular, angular to daedaloid; spores smooth, variously shaped and colored; cystidia and setae present or absent.

The genus *Fomes* contains all large perennial plants (except *Ganoderma*) with ungulate or applanate fruiting bodies. Exceptions to this, however, may be found in *F. ohiensis* and *F. scutellatus,* in which the fruiting bodies rarely exceed 3 cm. in breadth.

Fomes differs from *Ganoderma* chiefly in the presence of a thick shining or dull crust and spined spores in the latter. The fruiting bodies of some species of *Trametes* at times may be perennial and have stratified tube-layers; however, these fruiting bodies are never *Fomes*-like in structure, or never large and massive and not usually ungulate. Members of the genus *Daedalea* and *Lenzites* may be perennial, but they never have stratified tube- or lamellae-layers.

KEY TO THE SPECIES[71]

Context white, whitish, or very light yellowish-brown; setae never present; cystidia present or absent..1

Context darker than the above, wood-brown, dark yellowish-brown to brown; setae present or absent; cystidia never present......................4

[71] See footnote, p. 318.

Context of a definite rose-color. 9
1. Plants growing on living or dead *Shepherdia;* pileus with a reddish tinge when young, blackish when older. . . . . *53. F. fraxinophulis* f. *Ellisianus*
Plants growing on hosts other than *Shepherdia*. 2
2. Pileus not more than 2 cm. thick; usually effused-reflexed with a very narrow reflexed part. . . . . *54. F. annosus*
Pileus thicker than the above. 3
3. Mouths averaging (1)2–3 per mm.; plants growing only on species of *Juniperus*. . . . . *51. F. Demidoffii*
Mouths averaging 4–5 per mm.; plants growing on various coniferous and deciduous hosts. . . . . *45. F. pinicola*
4. Pileus with a thick horny crust; spores brown, minutely spined, truncate; no setae. . . . . *44. Ganoderma applanatum*
Pileus not heavily incrusted; spores smooth, hyaline or yellowish; setae present. 5
5. Context containing a thin black line less than 1 mm. broad. 6
Context not containing a black line as above. 7
6. Plants confined to coniferous hosts. . . . . *47. F. nigrolimitatus*
Plants confined to deciduous hosts. . . . . *50. F. conchatus*
7. Growing only on living or dead conifers; pileus dark brown to blackish . . . . *46. F. Pini*
Growing only on deciduous hosts; context dark reddish-brown. 8
8. Growing only on species of *Prunus;* mouths averaging 5–6 per mm.; producing a brown rot. . . . . *49. F. fulvus*
Growing on various deciduous hosts, especially aspen; mouths averaging 3–4 per mm.; producing a white rot. . . . . *48. F. igniarius*
9. Sporophores ungulate. . . . . *52. F. roseus*
Sporophores dimidiate to conchate. . . . . *43. Trametes subrosea*

1. Cystidia present and needle-like; setae absent.

45. Fomes pinicola (Sw.) Cooke, Grevillea **14:** 17. 1885.
Boletus ungulatus Schaeff. Fung. Bavar. **4:** 88. *pl. 137, 138.* 1774.
Boletus fulvus Schaeff. *ibid.* 89. *pl. 262.* Not *Boletus fulvus* Scop. 1772.
Boletus semiovatus Schaeff. *ibid.* 92. *pl. 270.*
Boletus marginatus Pers. Obs. Myc. **2:** 6. 1799.
Boletus pinicola Sw. Sv. Vet.-Akad. Handl. **1810:** 88. 1810.
Polyporus marginatus (Pers.) Fries, Syst. Myc. **1:** 372. 1821.
Polyporus pinicola (Sw.) Fries, *ibid.*
Fomes marginatus (Pers.) Gill. Champ. Fr. **1:** 683. 1878.
Fomitopsis pinicola (Sw.) Karst. Rev. Myc. **3**[9]: 18. 1881.
Fomes ungulatus (Schaeff.) Sacc. Syll. Fung. **6:** 167. 1888.
Ungulina marginata (Pers.) Pat. Ess. Tax. Hymen. p. 103. 1900.

Fomes ponderosus von Schrenk, U. S. Dept. Agr. Bur. Pl. Ind. Bull. 36: 30. 1903.

Plates 33, 34, figs. 1–2.

Pileus sessile, sometimes entirely resupinate, ungulate or applanate, woody, 3–20 x 3–20 x 1–10 cm.; surface glabrous, sometimes powdery, pelliculose or anoderm, usually sulcate, Light Buff to Pale Yellow-Orange when young, later Apricot Buff, Pecan Brown to almost black, often resinous when found on conifers; margin at first rounded, later obtuse and frequently of a lighter color than the rest of the pileus, often sterile below; context in young plants up to 4 cm. thick, in old specimens 1–5 mm. thick, corky to woody, white to Light Buff, hyphae of the context brownish under the microscope, unbranched, thick-walled, sometimes incrusted, 5–7 μ in diameter; tubes 2–5 mm. long each season, Light Buff, Pinkish Buff, to Cinnamon; mouths round, white, Maize Yellow to Light Buff, sometimes Wax Yellow, decidedly yellow-brown where bruised, averaging 4–5 per mm.; dissepiments 120–160 μ thick; trama golden under the microscope, occasionally containing brown crystalline bodies; hymenium 18–22 μ thick, loosely arranged; basidia 4-spored, 6–7 μ broad; spores hyaline, smooth, ovoid, 6–8 x 4–5 μ; hair-like cystidia usually present, 3–4 μ in diameter at their bases and tapered to a sharp point, extending up to 30 μ beyond the general level of the hymenium.

Habitat: parasitic and saprophytic on all conifers; occasionally found on *Populus tremuloides*.

Distribution: from the foothills up to the subalpine zone. Widespread in the United States.

Occurrence: very common. Throughout the year.

Type of rot: cubical brown rot.

Very young specimens of this fungus are almost globose, of a light yellow color, and often devoid of a hymenium, but later become sulcate, ungulate, or applanate, and of a darker color. Sporophores collected from coniferous hosts usually are covered with a sticky resinous exudation. This exudation, however, is never found on specimens from aspen. Occasionally, the fungus is entirely resupinate.

The needle-like cystidia are present only in mature hymenia

and entirely absent in young ones. In some cases, when KOH solution is applied to the tubes, they change to a reddish-brown color. This test, however, is not an infallible specific demarcation. Schmitz[72] suggests that various strains of this fungus probably exist in nature.

2. Setae present, cystidia absent.

A. Setae always present and abundant.

46. Fomes Pini (Thore) Lloyd, Synop. Fomes, p. 275. 1915.
Boletus Pini Thore, Chlor. Land. p. 487. 1803; Brot. Fl. Lusit. **2**: 468. 1804.
Daedalea Pini (Thore) Fries, Syst. Myc. **1**: 336. 1821.
Polyporus Pini (Thore) Pers. Myc. Eur. **2**: 83. 1825.
Trametes Pini (Thore) Fries, Epicr. Myc. p. 489. 1838.
Fomes Abietis Karst. Bidr. Finl. Nat. Folk **37**: 242. 1882.
Polyporus piceinus Peck, Ann. Rept. N. Y. State Mus. **42**: 25. 1889.
Trametes Pini Abietis Karst. Finl. Basidsv. p. 336. 1889.
Polystictus piceinus (Pk.) Sacc. Syll. Fung. **9**: 187. 1891.
Porodaedalea Pini (Thore) Murr. Bull. Torr. Bot. Club **32**: 367. 1905.

Plate 32, figs. 2–3.

Sporophores normally perennial, woody, ungulate to conchate, sessile, effused-reflexed or resupinate, often imbricate, confluent, 1–15 x 1–30(60) x 0.5–15 cm.; surface rough, sulcate, zonate, becoming rimose with age, hirsute, tomentose to glabrous, Argus Brown, Burnt Umber to black; margin rounded to acute, usually sterile below, velvety-tomentose, concolorous with the surface or more often lighter-colored as: Amber Brown to Brussel's Brown; context woody, usually less than 5 mm. thick, homogeneous, rarely zonate, Amber Brown to Argus Brown, hyphae of the context brownish under the microscope, rarely branched, 3–5 μ in diameter; tubes indistinctly stratified, usually stuffed in the older layers, rarely so in the new layers, 2–10 mm. long each season, concolorous with the context in older specimens, in young specimens Clay Brown to Wood Brown within; mouths circular,

[72] Schmitz, H. Am. Jour. Bot. 12: 163–176. 1925.

angular, or daedaloid, often of unequal diameter, 2–5 per mm., Wood Brown, Antique Brown, to Argus Brown; dissepiments very thin, 250 μ or more; hymenium hyaline under the microscope, 16–22 μ thick; basidia small, 4 μ broad; spores at first hyaline but turning light brown when mature, smooth, globose, 4–5 μ, or subglobose, 4–5(6) x 3.5–4 μ; setae abundant, pointed, projecting up to 20–30 μ beyond the hymenium, 8–12 μ in diameter.

Habitat: parasitic and saprophytic on conifers; rare on *Crataegus.*

Distribution: montane and subalpine zones. Widespread in the United States.

Occurrence: common. Throughout the year.

Type of rot: white rot.

As might be expected, one-year-old specimens of this fungus are more brightly colored than older ones. Due to this difference in appearance, the annual plants have previously been placed in *Fomes Abietis, Trametes Pini Abietis,* and *Polyporus* (*Polystictus*) *piceinus;* however, in the light of our present knowledge, these names should be considered conspecific. This species is sometimes called *Trametes Pini,* but since it develops into a large ungulate plant, it is thought advisable to consider it as a *Fomes.*

Compare *Fomes nigrolimitatus,* which has a black line at the base of its tube-layer, and *Trametes isabellina,* which has a light chocolate-colored pore layer. All of the above three plants have abundant setae in their hymenia.

47. Fomes nigrolimitatus (Romell) Egeland, Nyt Mag. **52:** 135. 1914.

Polyporus nigrolimitatus Romell, Arkiv f. Bot. **11**^{3}: 18. *pl. 1, f. 3.* 1911.

Phellinus nigrolimitatus (Romell) Bourd. & Galz. Hymen. Fr. 1: 622. 1927.

Plate 38, figs. 2–3.

Pileus corky, effused-reflexed, most frequently entirely resupinate, 1–5 x 4–20 x 1–5 cm., when entirely resupinate up to 30 x 60 cm.; surface at first soft, azonate, tomentose, anoderm, with age becoming woody, indistinctly zonate, and covered with

a thin brittle pellicle, at first Hazel to Bay, fading with age to Ochraceous-Tawny or almost black; margin acute to rounded, tomentose, Bay, sterile below; context soft and spongy, Kaiser Brown to Bay, 0.2–5 cm. thick, containing a thin black line less than 1 mm. thick and approximately 1 mm. above the tubes, context adjacent to the tubes lighter in color than the rest of the context, hyphae brown under the microscope, sparingly branched, 3–8 μ in diameter; tubes at length stratified, strata may be separated from each other by a narrow band of context about 1 mm. thick and containing a thin black line, or more frequently the tube-layers are stratified without the interception of layers of context, 0.2–2 cm. long each season, Sudan Brown to Brussels Brown, yellowish within; mouths circular to angular, concolorous with the tubes or in weathered specimens slightly darker, averaging 4–6 per mm.; dissepiments 60–100 μ broad; hymenium hyaline, made up of loosely arranged hyphae, 18–22 μ broad; basidia hyaline, 5–7 μ broad; spores hyaline, smooth, cylindric to elongate-ovoid, 6–8 x 2–3 μ; setae abundant, pointed, 8–10 μ broad, projecting up to 35 μ.

Habitat: on conifers, especially *Picea Engelmanni.*

Distribution: montane and subalpine zones. At the present time, known only from the Rocky Mountain region in the United States.

Occurrence: common. Throughout the year.

Type of rot: white pocket rot.

Of the various pore fungi found on coniferous hosts, the black line in the context and the abundant setae distinctly mark this plant. In most cases, the black line is so narrow that it can be seen only with the aid of a hand lens. The fruiting bodies most frequently found have only a single layer of tubes, and are almost always resupinate. Rarely is the species found with a narrowly reflexed margin. Compare with *Fomes conchatus* which is found only on deciduous hosts.

The type collection of *Fomes putearius* likewise has a black line in a similar position in the context and the plant looks very much like *F. nigrolimitatus.* Hubert[73] is of the opinion that these two species are conspecific, but Overholts[74] reports that the spores of

[73] Hubert, E. E. Jour. Agr. Res. 29: 528. 1924; Outline of forest pathology. p. 381. 1931.

[74] Overholts, L. O. Mycologia 23: 127. 1931.

F. putearius are hyaline, subglobose, 4–5 × 3–4 μ; hence they are markedly different in shape and size from those of *F. nigrolimitatus*, which are cylindric to elongate-ovoid, 6–8 × 2–3 μ. The writer has examined the type collection of *F. putearius*, but he was unable to find spores.

B. Setae not abundant, sometimes apparently absent.

48. **Fomes igniarius** (L.) Gill. Champ. Fr. **1**: 687. 1878.
Boletus igniarius L. Sp. Pl. p. 1176. 1753.
Polyporus igniarius (L.) Fries, Syst. Myc. **1**: 375. 1821.
Polyporus nigricans Fries, *ibid.*
Polyporus hyperboreus Berk. Ann. & Mag. Nat. Hist. **7**: 453. 1841.
Polyporus Novae-Angliae Berk. & Curt. Grevillea **1**: 51. 1872.
Fomes nigricans (Fr.) Gill. Champ. Fr. **1**: 685. 1878.
Phellinus igniarius (L.) Quél. Ench. Fung. p. 172. 1886.

Plate 35.

Pileus ungulate, rarely applanate, sessile or occasionally resupinate, 1–10 x 2–20 x 1–12 cm.; surface at first smooth, with age becoming distinctly rimose, incrusted, zonate, hirsute to glabrous, grayish-black to black; margin obtusely rounded, sterile below, hirsute-tomentose, not rimose, Ochraceous-Tawny to Sudan Brown, rarely grayish; context usually less than 1 mm. thick, concolorous with the surface, hyphae of the context dark-brown under the microscope, rarely branched, 3–4 μ in diameter; tube-layers stratified and forming the bulk of the fruiting body, tubes conspicuously white-stuffed in the older layers, 1–5 mm. long each season, Chestnut to Bay; mouths circular, 3–4 per mm., Bay to Chestnut, rarely grayish; dissepiments 40–90 μ thick; hymenium thin, hyaline, 8–10 μ thick; spores smooth, hyaline, subglobose to ovoid, 6–7 x 3–4 μ, abundant; setae infrequent, sometimes apparently absent, pointed, projecting 12–16 μ beyond the hymenium, 6–8 μ broad at their bases.

Habitat: on living and dead deciduous hosts, especially *Populus tremuloides;* rare on *Picea.*

Distribution: montane zone. Widespread in the United States.

Occurrence: common. Throughout the year.

Type of rot: white rot.

This fungus is closely related to *Fomes fulvus* in that the microscopical characters of the two plants are apparently similar. However, they can be conveniently separated as follows: *Fomes igniarius* causes a white rot and is found mainly on species of *Populus*, whereas *F. fulvus* causes a brown rot and is found only on species of *Prunus*.

Fomes igniarius attacks living aspen trees and, according to Meinecke,[75] causes an appreciable damage in certain parts of Colorado.

49. **Fomes fulvus** (Scop.) Gill. Champ. Fr. **1**: 687. 1878.
Boletus fulvus Scop. Fl. Carn. ed. 2. **2**: 469. 1772. Not *Boletus fulvus* Schaeff. 1774.
Boletus pomaceus Pers. Obs. Myc. **2**: 5. 1799.
Polyporus pomaceous Pers. Myc. Eur. **2**: 84. 1825.
Polyporus fulvus (Scop.) Fries, Epicr. Myc. p. 466. 1838.
Placodes pomaceus (Pers.) Quél. Fl. Myc. Fr. p. 399. 1888.
Placodes fulvus (Scop.) Quél. *ibid.*
Pyropolyporus fulvus (Scop.) Murr. Bull. Torr. Bot. Club **30**: 112. 1903.
Fomes pomaceus (Pers.) Big. & Guill. Fl. Champ. Fr. **2**: 355. 1913.

Plate 34, figs. 4–6.

Pileus dimidiate to ungulate, occasionally imbricate, sessile, effused-reflexed, rarely resupinate, 1–10 x 2–15 x 1–6 cm.; surface at first smooth, with age becoming more or less rimose and incrusted, indistinctly zonate, hirsute to glabrous, Hair Brown to Deep Mouse Gray; margin obtusely rounded, sterile below, hirsute-tomentose, not rimose, Ochraceous-Tawny to Sudan Brown; context 1–5 mm. thick, concolorous with the surface, hyphae of the context dark-brown under the microscope, rarely branched, 3–4 μ in diameter; tube-layers stratified, forming the bulk of the fruiting body, tubes in the older strata occasionally white-stuffed but not markedly so, 1–5 mm. long each season, Chestnut to Bay; mouths circular, (4)5–6 per mm., Bay to Chestnut Brown; dissepiments 40–90 μ thick; hymenium thin and

[75] Meinecke, E. P. U. S. Dept. Agr., Tech. Bull. 155. 1929.

hyaline, 8–10 μ thick; spores smooth, hyaline, subglobose to ovoid, 6–7 x 3–4 μ; setae infrequent, sometimes apparently absent, pointed, projecting 12–16 μ beyond the hymenium, 6–7 μ broad at their bases. Spores and setae are the same as those in *Fomes igniarius*.

Habitat: on various species of the genus *Prunus*.

Distribution: montane zone. Widespread in the United States.

Occurrence: rare. Summer and autumn.

Type of rot: brown rot.

See page 383 for a discussion of this species and its comparison with *Fomes igniarius*.

50. Fomes conchatus (Pers.) Gill. Hymen. Fr. p. 685. 1874.
Boletus salicinus Pers. in Gmel. Syst. Nat. **2:** 1437. 1791. Not *Boletus salicinus* Bull. 1789.
Boletus conchatus Pers. Obs. Myc. **1:** 24. 1796.
Polyporus conchatus (Pers.) Fries, Syst. Myc. **1:** 376. 1821.
Polyporus salicinus (Pers.) Fries, *ibid.*
Polyporus loricatus Pers. Myc. Eur. **2:** 86. 1825.
Phellinus salicinus (Pers.) Quél. Fl. Myc. Fr. p. 394. 1888.
Pyropolyporus conchatus (Pers.) Murr. Bull. Torr. Bot. Club **30:** 117. 1903.

Pileus woody, rigid, effused-reflexed with the reflexed portion conchate, broadly effused and often entirely resupinate, 0–6 x 3–10 x 0.3–2 cm.; surface tomentose, irregularly sulcate, anoderm, Auburn to Mars Brown, with age becoming incrusted and almost black; margin acute, undulating, tomentose, Tawny to concolorous, sterile below; context woody, usually very thin, 0.5–3 (8) mm. thick, indistinctly zonate, containing one to several black lines less than 1 mm. in thickness, Antique Brown, hyphae brown under the microscope, thick-walled, with few septa, 1.5–4 μ in diameter; tubes concolorous with the context, at length stratified, 0.5–4 mm. long each season; mouths circular, 5–7 per mm., Antique Brown to Sudan Brown; dissepiments 35–50 μ broad; hymenium hyaline, narrow, 6–10 μ broad; basidia hyaline, 4–6 μ in diameter; spores hyaline, smooth, sugblobose to ovoid, 4–6 x 4–5 μ; setae ventricose, 6–10 μ broad at their bases, projecting 10–20 μ beyond the hymenium, never extremely numerous and often somewhat

rare in occurrence, similar in shape to those of *F. igniarius* and *F. fulvus*.

Habitat: on various deciduous hosts.

Distribution: montane and subalpine zones. Somewhat widespread in the United States.

Occurrence: rare. Summer and autumn.

Type of rot: white rot.

This species was collected only once in Colorado, and this collection was made by Baker, Earle, and Tracy in 1898.[76]

Fomes conchatus is usually a thin plant and scarcely has the appearance of a *Fomes;* it is often entirely resupinate, and the context contains one to several thin black lines that can be seen only with the aid of a hand lens. As to color, growth-form, and presence of a black line in the context, this fungus is similar to *Fomes nigrolimitatus*. The latter species, however, differs in host relations, in the size, shape, and abundance of the setae, and in the size and shape of the spores.

3. Neither cystidia nor setae present in the hymenium.

A. Spores yellowish-colored and markedly truncate.

51. Fomes Demidoffii (Lév.) Sacc. & Sydow, in Sacc. Syll. Fung. **6**: 189. 1888.

Polyporus Demidoffii Lév. in Demid. Voy. Russ. Merid. **2**: 92. 1842; *ibid.* Atlas Crypt. *pl. 3.* 1842.

Polyporus Juniperinus von Schrenk, U. S. Dept. Agr. Bull. Veg. Phys. 21: 9. 1900.

Fomes Juniperinus (von Schrenk) Sacc. & Sydow, in Sacc. Syll. Fung. **16**: 151. 1902.

Pyropolyporus Juniperinus (von Schrenk) Murr. Bull. Torr. Bot. Club **30**: 116. 1903.

Pyropolyporus Earlei Murr. *ibid.*

Fomes Earlei (Murr.) Sacc. & D. Sacc. in Sacc. Syll. Fung. **17**: 119. 1905.

Fulvifomes Juniperinus (von Schrenk) Murr. North. Polyp. p. 501. 1914.

Plate 34, fig. 3.

[76] Greene, E. L. Plantae Bakerianae **1**: fasc. 1, p. 24. 1901.

Pileus woody, ungulate, 3–10 x 3–12 x 3–15 cm.; surface at first tomentose, yellowish-brown, zonate, at length becoming glabrous, Sepia to blackish, rimose; margin rounded, tomentose, at first Warm Buff, with age and on bruising becoming Amber Brown; context zonate, Amber Brown to Kaiser Brown, 3–10 mm. thick, hyphae of the context brown under the microscope, thick-walled, apparently aseptate, rarely branched, 3–4 μ in diameter; tubes indistinctly stratified, concolorous with the context, 5–10 mm. long each season; mouths angular to irregular, (1)2–3 per mm., concolorous with the tubes; dissepiments 125–175 μ thick; hymenium yellowish-brown under the microscope, loosely arranged, indistinctly delimited from the trama, 35–40 μ broad; basidia yellowish-brown, 7–8 μ broad; spores smooth, yellowish-brown, ovoid, truncate, 6–8 x 4–5 μ, copious; typical cystidia absent, large, club-shaped bodies, which are considered as immature basidia, frequently abundant.

Habitat: confined to living and dead members of the genus *Juniperus*.

Distribution: plains and foothill zones. Widespread in the United States.

Occurrence: common. Throughout the year.

Type of rot: white rot.

According to Lloyd,[77] Murrill,[78] Seymour,[79] and Bourdot and Galzin,[80] *Fomes Demidoffii* is not distinct from *F. Juniperinus*. Since the former name is the older one, it is advisable to employ it here.

Even though Hedgcock and Long[81] have pointed out the fact that *Fomes Earlei* and *F. Juniperinus* produce slightly different rots and have pores of different size, the writer is of the opinion that these species are conspecific and that these differences may be attributed to the different hosts upon which the fungi grow, and also to the different geographic locations of the collections of the rots and fruiting bodies.

Many collections of this fungus have been made in Colorado

[77] Lloyd, C. G. Mycol. Notes **4**: 522. 1912; Syn. Fomes, p. 232. 1915.

[78] Murrill, W. A. Mycologia **12**: 14. 1920.

[79] Seymour, A. B. Host Index, p. 76. 1929.

[80] Bourdot, H. & A. Galzin. Hymen. Fr. **1**: 689. 1927.

[81] Hedgcock, G. G. & W. H. Long. Mycologia **4**: 109–114. 1912.

by Hedgcock on junipers found on dry bluffs and mesas of the foothill zone. Its occurrence, however, is not coextensive with that of the hosts; on the contrary, the fungus is found on widely scattered groups of junipers.

B. Spores hyaline, truncate or not truncate.

a. Spores allantoid.

52. **Fomes roseus** (Alb. & Schw.) Cooke, Grevillea **14**: 21. 1885.

Boletus roseus Alb. & Schw. Consp. Fung. p. 251. 1805.

Polyporus roseus (Alb. & Schw.) Fries, Syst. Myc. **1**: 372. 1821.

Polyporus rufo-pallidus Trog, Flora **15**: 556. 1832.

Fomitopsis rosea (Alb. & Schw.) Karst. Rev. Myc. **3**^{9}: 18. 1881.

Ungulina rosea (Alb. & Schw.) Pat. Ess. Tax. Hymen. p. 103. 1900.

Plate 29, figs. 4–6.

Pileus coriaceous-woody, sessile, effused-reflexed, ungulate, 1–5 x 1–6 x 1–4 cm.; surface anoderm, sulcate, rimose, tomentose to nearly glabrous, Fuscous-Black to black; margin round, Natal Brown to concolorous, sterile below; context 0.5–2 cm. thick, corky-firm, indistinctly zonate, Shell Pink to Vinaceous Pink, hyphae of the context yellowish-brown under the microscope, sparingly branched, thick-walled, apparently aseptate, 3–5 μ in diameter; tubes concolorous with the context, stratified, white-stuffed in the older strata, white-lined in the younger ones, 1–3 mm. long each season; mouths concolorous or slightly darker in weathered specimens, round to slightly angular, 3–5 per mm.; dissepiments 60–140 μ thick, yellowish-brown; hymenium hyaline, 14–18 μ thick; basidia hyaline, 5–6 μ in diameter, projecting up to 6 μ; spores hyaline, smooth, cylindric, rarely curved, 6–9 x 2–3 μ; no cystidia observed.

Habitat: on conifers.

Distribution: foothill, montane, and subalpine zones. Widespread in the United States.

Occurrence: rare. Autumn.

Type of rot: brown rot.

This fungus is separated from *Trametes subrosea* by its lighter rose-colored context and its ungulate growth-form. It is of rare occurrence in Colorado, and nowhere in the United States is it found in great abundance. Weir[82] reports it as occurring only on conifers.

b. Spores ovoid.

53. **Fomes fraxinophilus** forma **Ellisianus** (And.) Baxter, Am. Jour. Bot. **12:** 523. 1925.

Fomes Ellisianus Anderson, Bot. Gaz. **16:** 113. 1891.

Polyporus circumstans Morgan, Jour. Cinc. Soc. Nat. Hist. **18:** 37. 1895.

Plate 37, fig. 3.

Pileus woody, dimidiate, ungulate, 3–10 x 3–15 x 2–10 cm.; surface at first tomentose, radiate-rugose, Kaiser Brown to Bay, with age becoming rimose and blackish; margin obtuse to rounded, concolorous or lighter, as Pinkish Buff; context scanty, usually less than 5 mm. thick, Pinkish Buff to Warm Buff, hyphae of the context yellowish-brown under the microscope, very thick-walled, easily broken, with very few septa, apparently unbranched, 4–5 μ in diameter; tubes indistinctly stratified, concolorous with the context, 3–6 mm. long each season, slightly stuffed in the older strata; pores concolorous with the tubes, circular to subcircular, 2–4 per mm.; free edges of the dissepiments at first pruinose, with age becoming glabrous, 80–150 μ thick; hymenium hyaline, 12–16 μ thick; basidia hyaline, 7–8 μ broad; spores smooth, hyaline, ovoid, occasionally truncate, 7–8 x 5–6 μ; no cystidia observed.

Habitat: on living and dead *Shepherdia argentea*.

Distribution: plains and foothill zones. Rocky Mountain region.

Occurrence: abundant where the host occurs. Throughout the year.

Type of rot: white rot.

This fungus has the general appearance of both *Fomes fraxinophilus* and *F. Demidoffii*, but the latter two species have darker-

[82] Weir, J. R. Rhodora **25:** 214–220. 1923.

colored contexts and tubes. Baxter[83] has presented cultural and morphological characteristics of this fungus and *F. fraxinophilus*, and shows them to be closely related.

54. Fomes annosus (Fr.) Cooke, Grevillea **14**: 20. 1885.
Polyporus annosus Fries, Syst. Myc. **1**: 373. 1821.
Polyporus serpentarius Pers. Myc. Eur. **2**: 82. 1825.
Polyporus subpileatus Weinm. Syll. Pl. Nov. **2**: 102. 1827.
Polyporus resinosus Rostk. in Sturm, Deutsch. Fl. **4**:61. 1830. Not *Polyporus resinosus* (Schrad.) Fr. 1821.
Trametes radiciperda R. Hartig, Wicht. Krankh. Waldb. p. 62. 1874.
Fomitopsis annosa (Fr.) Karst. Rev. Myc. **3**[9]: 18. 1881.
Polyporus Gillotii Roum.; Gillot, Rev. Myc. **4**: 234. *pl. 32*. 1882.
Heterobasidion annosum (Fr.) Bref. Unters. Gesammt. Myk. **8**: 154. 1889.
Polyporus irregularis Underw. Bull. Torr. Bot. Club **24**: 85. 1897.
Ungulina annosa (Fr.) Pat. Ess. Tax. Hymen. p. 103. 1900.

Plate 36.

Sporophores resupinate, effused-reflexed, or sessile, woody, irregular in shape, usually conchate to applanate, 5–12 x 5–18 x 0.5–2 cm.; surface velvety to nearly glabrous, rugose, zonate, more or less incrusted, new growth Cinnamon-Buff to Clay Color, older growth Rood's Brown, Natal Brown to blackish; margin entire to wavy-lobed, acute, concolorous with the new growth, sterile below; annual tube-layers loosely cemented together at their margins; context 2–10 mm. thick, woody, white to Pale Ochraceous-Buff, upper part forming a hard, horny, and black or very dark brown pellicle, 0.2–0.3 mm. thick, hyphae below the pellicle hyaline, sparingly branched, 3–5 μ in diameter; tubes unevenly and indistinctly stratified, 2–6 mm. long each season, old tubes usually stuffed, white to Pale Ochraceous-Buff; mouths circular to angular, irregular and of unequal size, 2–3 per mm., white, Pale Ochraceous-Buff to Ochraceous-Buff; dissepiments

[83] Baxter, D. V. *l.c.*

becoming dentate with age, 60–100 μ thick; hymenium 10–15 μ broad, evanescent and often entirely absent; basidia hyaline, 4–7 μ broad; spores hyaline, smooth, ovoid, 4–6 x 3–4 μ; no cystidia observed.

Habitat: various coniferous hosts, especially *Picea Engelmanni;* rare on deciduous hosts.

Distribution: montane and subalpine zones. Widespread in the United States.

Occurrence: rare in Colorado; apparently frequent elsewhere.

Type of rot: white rot.

Although this fungus is of frequent occurrence in the United States, only one collection is known from Colorado. This was made at Cripple Creek, Colorado, on *Picea Engelmanni,* by Humphrey, in 1909. Undoubtedly, additional specimens will be found in later years.

One outstanding characteristic of *Fomes annosus* is the free edges of the annual layers of growth. This characteristic, which can be seen in plate 36, seems to be constant in occurrence. Also, the plant is rather thin for a *Fomes,* never exceeding 2 cm. in thickness.

Conidia production has been known since the time of Brefeld (1889). An illustration of these may be found in Gaümann and Dodge, *l. c.*, p. 446.

LENZITES

Lenzites Fries, Gen. Hymen. p. 10. 1836.

Plants annual or perennial, lignicolous, sessile or effused-reflexed, coriaceous to woody, never putrescent; surface anoderm, usually zonate, tomentose; context white to brown, thin; hymenium disposed on radiating lamellae which at times become more or less transversely anastomosed; spores hyaline, smooth, cylindric, usually curved; cystidia present or absent; no setae.

Members of the genus *Lenzites* are somewhat similar in appearance to those of the gymnocarpous Agaricales, both of which have radiating lamellae or gills. Members of this genus, however, are always coriaceous or woody and never putrescent, whereas members of the Agaricales are usually fleshy and putrescent.

At times, young specimens of this genus may show a poroid or daedaloid condition of the hymenial elements, due to the presence

of transverse dissepiments. These dissepiments, however, usually break down with age, thus producing a true lamellate condition.

KEY TO THE SPECIES

Context white to whitish. 1
Context brown. 2
1. Pileus dark-brown; tubes or lamellae white to whitish. . . *38. Trametes variiformis*
Pileus gray to cinereous; lamellae brown or purplish. . . . . . *6. Polyporus abietinus*
Pileus white to whitish; lamellae white to yellowish. . *39. Trametes heteromorpha*
2. Pileus gray, cinereous to gray, never brown, less than 4 mm. thick. . . . . *6. Polyporus abietinus*
Pileus yellowish-brown to rusty-brown, more than 4 mm. thick. 3
3. Lamellae or pores large, averaging 1 per mm., usually lamellate from the first. . . . . *55. L. saepiaria*
Lamellae or pores smaller, 1–2 per mm., sometimes poroid to daedaloid . . . . *56. L. trabea*

55. Lenzites saepiaria (Wulf.) Fries, Epicr. Myc. p. 407. 1838.
Agaricus hirsutus Schaeff. Fung. Bavar. **1:** *pl. 76.* 1762.
Agaricus saepiarius Wulfen, in Jacq. Coll. **1:** 347. 1786.
Agaricus boletiformis Sow. Col. Figs. Eng. Fung. *pl. 418.* 1814.
Daedalea saepiaria (Wulf.) Fries, Obs. Myc. **1:** 105. 1815.
Lenzites rhabarbarina Berk. & Curt. Ann. & Mag. Nat. Hist. II. **12:** 438. 1853.
Sesia hirsuta (Schaeff.) Murr. Jour. Myc. **9:** 88. 1903.
Gloeophyllum hirsutum (Schaeff.) Murr. Jour. Myc. **9:** 94. 1903. In part.
Gloeophyllum abietinellum Murr. N. Am. Fl. **9:** 129. 1908.
Lenzites abietinella (Murr.) Sacc. & Trott. in Sacc. Syll. Fung. **21:** 126. 1912.

Plate 37, figs. 1–2.

Pileus annual or perennial, flabelliform, dimidiate or conchate, sessile or effused-reflexed, 1–5 x 2–15 x 0.3–1 cm.; surface zonate, strigose, anoderm, uneven, Argus Brown, Bone Brown to almost black; margin even to undulating, at first round, strigose-tomentose, sterile below, Ochraceous-Tawny, with age becoming acute, fertile, concolorous with the surface; context homogeneous to indistinctly zonate, corky, Ochraceous-Tawny, turning with age to Argus Brown, 2–6 mm. thick, hyphae of the context radially arranged, brown under the microscope, sparingly branched,

straight, with few cross walls, thin-walled, 4–6 μ in diameter; lamellae occasionally anastomosing, Light Ochraceous-Buff to Ochraceous-Orange, 0.5–1 mm. broad, 2–10 mm. deep, averaging about 1 per mm., edges at first thick, hirsute, entire, with age becoming thin, glabrous, dentate-lacerate; hymenium hyaline, 22–30 μ broad; basidia hyaline, 4–5 μ in diameter; spores hyaline, smooth, elongate-ellipsoid, occasionally curved, apiculate, 8–10 x 3–4 μ; cystidia small and inconspicuous, hyphae-like with incrusted apexes, projecting up to 10 μ, similar in structure to those of *Polyporus abietinus* (pl. 18, fig. 5).

Habitat: on various conifers; rare on deciduous hosts.

Distribution: widespread in Colorado and the United States.

Occurrence: common. Throughout the year.

Type of rot: brown rot.

This fungus is the most common one found in Colorado. It grows upon all conifers irrespective of altitude, and is occasionally found on aspen (*Populus tremuloides*) and rarely on alder (*fide* Kauffman, *l. c.*, reported as *Lenzites abietinella*). It is easily identified by its brownish pileus with an orange-colored margin, and its thick lamellae.

It was thought by Murrill[84] and others that *Trametes odorata* (*T. protracta*) was the poroid form of this species. However, Snell *et al.*[85] have recently established the validity for separating these two species.

Lenzites abietinella, which was described from plants collected in Colorado, has smaller and more closely set lamellae than is shown in typical specimens of *L. saepiaria* (pl. 37). Intermediate stages, however, have been found, hence this species is considered here as one of the many variants. The European *Lenzites abietina* is also closely related, but due to the presence of ventricose cystidia, it is sufficiently distinct to carry a specific name.

56. Lenzites trabea (Pers.) Fries, Epicr. Myc. p. 406. 1838.
Agaricus trabeus Pers. Syn. Fung. **1:** xxix. 1801.
Daedalea trabea (Pers.) Fries, Syst. Myc. **1:** 335. 1821.
Lenzites vialis Peck, Ann. Rept. N. Y. State Mus. **26:** 67. 1874.

[84] Murrill, W. A. Mycologia **12:** 15. 1920.
[85] Snell, W. H. *et al.* Mycologia **20:** 276–291. 1928.

Sesia pallidofulva Murr. Bull. Torr. Bot. Club **31**: 605. 1904.
Gloeophyllum pallidofulvum Murr. *ibid.* **32**: 370. 1905.
Gloeophyllum trabeum (Pers.) Murr. N. Am. Fl. **9**: 129. 1908.

Plate 38, fig. 1.

Pileus coriaceous, sessile, effused-reflexed, occasionally resupinate, dimidiate, laterally connate, 1–4 x 1–7 x 0.2–1.5 cm.; surface tomentose to nearly glabrous, smooth to tuberculate, zonate, Sayal Brown, Cinnamon-Brown to Mummy Brown; margin entire to undulating, obtuse, tomentose, concolorous to lighter, sterile below; context soft-corky, Sayal Brown to Cinnamon-Brown, homogeneous, with age becoming indistinctly multizonate and duplex, the layer adjacent to the tubes lighter-colored and firmer, 1–6 mm. thick, hyphae of the context of two kinds: hyaline hyphae 2–3 μ in diameter, and brown hyphae 4–6 μ in diameter; tubes or lamellae concolorous with the context, fulvous lined, 2–12 mm. long; mouths poroid, daedaloid, labyrinthiform, or radially elongate to lamellate, 1–2 per mm., Ochraceous-Tawny to Cinnamon-Brown; dissepiments undulating, dentate to lacerate, often torn, usually very thin, 40–80(150) μ thick; hymenium hyaline, 16–25(35) μ broad; basidia hyaline, 4–6 μ in diameter, usually projecting up 20 μ beyond the level of the hymenium; spores hyaline, smooth, cylindric to elongate-ellipsoid, apiculate, 8–12 × 3–4.5 μ; no cystidia observed.

Habitat: on both coniferous and deciduous hosts, especially cottonwoods (*Populus* spp.).

Distribution: plains and foothill zones. Northeastern United States and the Rocky Mountain region.

Occurrence: uncommon. Spring and summer.

Type of rot: brown rot.

This fungus may be found in all stages of development from a typical poroid to a typical lamellate condition, hence identification at times is bothersome. The poroid form may be confused with *Trametes odorata,* and the lamellate form with *Lenzites saepiaria;* but in the latter two species, the dissepiments are nearly 1 mm. thick, whereas those of *L. trabea* are paper-thin.

FAVOLUS

Favolus Beauv. Fl. Oware **1:** 1. *pl. 1.* 1805.

Plants annual, lignicolous, fleshy-tough when fresh; stipe short, lateral, rarely excentric, rarely sessile; context white, thin; pore-mouths large, angular, alveolar, radially elongated, often radially arranged; spores hyaline; no cystidia.

The members of this genus are characterized by the presence of large radially elongated pores, which are usually radially arranged, and the lateral short stipe. The genus differs from *Hexagona* in that the pores of specimens of the latter genus are hexagonal or honey-comb-like in structure. Furthermore, *Hexagona* is a tropical genus, whereas *Favolus* is both tropical and temperate in distribution.

57. Favolus alveolaris (DC.) Quél. Ench. Fung. p. 185. 1886.
Merulius alveolaris DC. Fl. Fr. **6:** 43. 1815.
Hexagona Mori Pollini, Pl. Nov. p. 35. 1816.
Cantharellus alveolaris (DC.) Fries, Syst. Myc. **1:** 322. 1821.
Boletus arcularius Schw. Schr. Nat. Ges. Leipzig **1:** 95. 1822. Not *Boletus arcularius* Batsch. 1783.
Favolus canadensis Klotzsch, Linnaea **7:** 197. 1832.
Favolus europaeus Fries, Epicr. Myc. p. 498. 1838.
Polyporus Boucheanus peponinus Berk. & Curt. Ann. & Mag. Nat. Hist. II. **12:** 432. 1853.
Favolus ohiensis Berk. & Mont.; Mont. Syll. Crypt. p. 171. 1856.
Favolus striatulus Ellis & Ev. Am. Nat. **31:** 339. 1897.
Hexagona alveolaris (DC.) Murr. Bull. Torr. Bot. Club **31:** 327. 1904.
Hexagona micropora Murr. *ibid.* 328.
Hexagona striatula (Ellis & Ev.) Murr. N. Am. Fl. **9:** 48. 1907.

Plate 38, fig. 5.

Pileus reniform, flabelliform to circular, convex-plane, depressed behind, fleshy-tough when fresh, drying brittle, 1–4 x 1–8 x 0.2–0.7 cm.; surface at first strigose-squamose, Mars Yellow to Ochraceous-Tawny, at length almost glabrous and fading to Light

Buff; margin at first thin, entire, incurved, at length becoming thicker, undulating to lobed, concolorous, or as dark as Chestnut-Brown; context homogeneous, 0.5–2 mm. thick, white in fresh plants, drying Light Buff to Ochraceous-Tawny, hyphae of the context hyaline under the microscope, branched, 3–5 μ in diameter; tubes decurrent, at first white to Light Buff, drying Light Vinaceous-Cinnamon to Russet, 1–5 mm. long; mouths concolorous, radially elongated, 2–5(10) mm. long, 1–2.5 mm. broad, radially arranged; dissepiments thin, often torn so that the pores are confluent and lamellae-like, dentate, 150–400 μ thick; stipe lateral, rarely excentric, short, usually a lateral tubercle, 2–8 mm. thick, 1–12 mm. long, concolorous with the surface of the pileus; hymenium hyaline, compact, 22–26 μ broad; basidia hyaline, 6–8 μ in diameter; spores smooth, hyaline, elongate-ellipsoid, apiculate, occasionally curved, 9–12 x 3–4.5 μ; no cystidia.

Habitat: on various deciduous hosts.

Distribution: foothill zone. Northern half of the United States and west as far as Montana and Colorado.

Occurrence: rare. Spring.

Type of rot: white rot.

Only a single collection of this fungus, made by E. Bethel, on choke cherry, near Boulder, Colorado, is known from Colorado.

The plant is characterized by its short lateral stipe and radially elongated pores. *Polyporus arcularius* may at times have radially elongated pores, but it differs from this species in having a central stipe and a ciliated margin.

In most of the American and foreign literature, this plant is named *Favolus europaeus*, or *F. canadensis*. The departure from "usage" is made in order to comply with the International Rules.

PORIA

Poria Pers. Neues Mag. Bot. **1:** 109. 1794.

Plants annual or perennial, lignicolous, resupinate, separable or inseparable; margin thin or thick, fertile or sterile; pores circular to daedaloid; spores variously shaped and colored; setae or cystidia present or absent.

The genus *Poria* contains all persistently resupinate members

of the family Polyporaceae. One occasionally finds species of *Polyporus*, *Trametes*, and *Fomes* which under unusual conditions complete their cycle of growth in a resupinate growth-form. This has lead to the description of several species of *Poria* which are only resupinate growth-forms of pileate species. For example, *Poria callosa* is *Trametes serialis*, and *Poria obducens* is *Fomes connatus*.

KEY TO THE SPECIES

Sporophores light-colored, as: white, cream, or yellow........................1
Sporophores dark-colored, as: brown, purple, or red........................4
1. Sporophores with a brownish-colored, sterile margin which is more than 1 mm. thick........................*58. P. monticola*
Sporophores with variously colored, sterile margins which are less than 1 mm. thick, or margins entirely fertile........................2
2. Margin either sterile to a breadth of 1 mm. or less, or else entirely fertile ....*59. P. vaporaria*
Margin usually sterile to a breadth of more than 1 mm........................3
3. Growing mainly on deciduous wood........................*60. P. medulla-panis*
Growing mainly on coniferous wood........................*61. P. subacida*
4. Sporophores some shade of red........................*62. P. spissa*
Sporophores some shade of purple........................*63. P. purpurea*
Sporophores ferruginous in color........................5
5. Spores 4.5–5 x 2–3 μ........................*64. P. ferruginosa*
Spores 6–9 x 2 μ........................*36. Trametes isabellina*

58. Poria monticola Murr. Mycologia **12**: 90. 1920.

Plate 38, fig. 4.

Sporophores widely effused, inseparable, 1–6 mm. thick; margin sometimes thin, fimbriate to membranous, fertile, more frequently thick, sterile, hirsute, darker than the pores, Prout's Brown, Mummy Brown to Blackish Brown; subiculum less than 1 mm. thick, white to Cartridge Buff, hyphae hyaline under the microscope, branched, with few septa, very thick-walled, 3–4 μ in diameter; tubes 1–5 mm. long, often oblique and laterally opened, at first white, with age and on drying becoming Light Buff to Warm Buff; mouths angular to elongate, averaging 2–3 per mm., at first white, drying Light Buff to Warm Buff, brownish and translucent where bruised; dissepiments entire to dentate, 75–150 μ thick; hymenium hyaline under the microscope, 12–16 μ broad; basidia hyaline, 5–7 μ in diameter; spores hyaline, smooth, elongate-ellipsoid, occasionally curved, 5–7 x 2–3 μ; no cystidia observed.

Habitat: on both coniferous and deciduous hosts.

Distribution: montane zone. Known from Idaho and Colorado.

Occurrence: rare. Summer and autumn.

Type of rot: white rot.

This *Poria* is characterized by having a thick, dark-brown, sterile margin which gives the impression that the fruiting body is slightly reflexed.

59. Poria vaporaria (Fr.) Cooke, Grevillea **14:** 111. 1886. Not *Poria vaporaria* Pers. 1797.

Polyporus vaporaria Fries, Obs. Myc. **2:** 260. 1818; Syst. Myc. **1:** 382. 1821.

Boletus incertus Pers. Myc. Eur. **2:** 106. 1825.

Poria incerta (Pers.) Murr. Mycologia **12:** 78. 1920.

Plate 39, fig. 2.

Sporophores widely effused, inseparable, the white floccose mycelium penetrating into the wood and perceptible to the unaided eye, 0.5–1.5 mm. thick; margin at first sterile to a breadth of 1 mm. or less, white, floccose, with age becoming fertile; subiculum less than 1 mm. thick, apparently absent in old specimens; tubes 0.5–1.5 mm. long, often oblique, at first white, with age and on drying turning Pinkish Buff, Warm Buff to Cinnamon-Buff, tubes often splitting apart in uneven lines and revealing the floccose underlying subiculum; mouths concolorous, circular to angular, never daedaloid, unequal, averaging 2–4 per mm.; dissepiments with age becoming denticulate; hyphae of the trama hyaline, nodose-septate, 2–3 μ in diameter; basidia 4–5 μ broad; spores hyaline, smooth, allantoid, 4–6 x 1–2 μ; no cystidia.

Habitat: on various coniferous and deciduous hosts.

Distribution: montane zone. Widespread in the United States.

Occurrence: rare. Autumn.

Type of rot: brown rot.

Only a single collection of this fungus is reported from Colorado. This was made by Seaver and Bethel at Tolland, Colorado, in 1910, and identified by Murrill. The writer has drawn the above description from this collection, and it agrees in its essential characters with the description of *Poria vaporaria* by Bourdot and Galzin.[86]

[86] Bourdot, H. & A. Galzin. Hymen. Fr. 1: 673. 1927.

There seems to be some confusion in the identity of this plant. Bourdot and Galzin (*l. c.*) state: "Cette plante n'est pas le *P. vaporaria* Pers. qui, d'après M. Bresadola, représenterait vraisemblablement le *P. Vaillantii* Fr.—La spore que figure Quélet (Ass. fr., 1891, f. 25) pour *P. vaporaria* est celle de *P. mucida* Pers. et, c'est sur des formes de cette dernière espèce, que tombaient toutes les déterminations qu'il nous a données de *P. vaporaria*. Cette interprétation de Quélet est du reste presque universellement suivie en France et en Angleterre." Murrill[87] has expressed somewhat the same idea as that just stated.

60. Poria medulla-panis (Jacq.) Pers. Neues Mag. Bot. **1:** 109. 1794; Syn. Myc. **2:** 544. 1801.

Boletus medulla-panis Jacquin, Misc. Austr. p. 141. *pl. 11.* 1778.

Polyporus medulla-panis (Jacq.) Fries, Syst. Myc. **1:** 380. 1821.

Polyporus xantholoma Schw. Trans. Am. Phil. Soc. II. **4:** 158. 1832.

Poria xantholoma (Schw.) Cooke, Grevillea **14:** 113. 1886.

Plate 39, fig. 4.

Sporophores annual or perennial, inseparable, 1–8 mm. thick, 5–30 cm. or more long; subiculose margin at first sterile to a breadth of 0.5–3 mm., obtusely rounded, thick, undulating, tomentose, Cream Color to Chamois, with age becoming fertile, acute, and as dark as Honey Yellow; subiculum less than 1 mm. thick, white to pallid, hyphae hyaline to yellow under the microscope, much branched and interwoven, incrusted, 1.5–3(5) μ in diameter; tubes indistinctly stratified, often oblique, the older layers white-stuffed, 0.5–3 mm. long each season; mouths concolorous with the margin, with age fading to almost white, circular to angular, 3–5 per mm.; large crystalline bodies often abundant in the trama, hyphae of the trama yellowish under the microscope; basidia hyaline, 5–8 μ in diameter; spores hyaline, smooth, broadly ellipsoid, occasionally truncate, 4–7 x 3–5 μ; no typical cystidia observed.

[87] Murrill, W. A. Mycologia 12: 78. 1920.

Habitat: on various deciduous hosts.

Distribution: foothill zone to subalpine zone. Widespread in the United States.

Occurrence: common. Summer and autumn.

Type of rot: white rot.

Poria medulla-panis and *P. subacida* are both yellowish-colored and have similar hymenial structures. They may be conveniently separated as follows: *P. medulla-panis* is found only on deciduous hosts, it has a thick sterile margin, and the hyphae of the subiculum are much branched, interwoven, and thin. *P. subacida* is found only on coniferous hosts; it has a thin sterile margin, and the hyphae of the subiculum are thick-walled and apparently unbranched.

61. Poria subacida (Pk.) Sacc. Syll. Fung. **6:** 325. 1888.

Polyporus subacida Peck, Ann. Rept. N. Y. State Mus. **38:** 92. 1885.

Plate 39, fig. 3.

Sporophores annual or perennial, separable to inseparable, 1–20 mm. thick, extended to a distance of 1 meter or more; subiculose margin at first sterile to a breadth of 0.5–6 mm., tomentose, irregular to arachnoid, acute, thin, Light Buff, Pinkish Buff to Ochraceous-Buff, with age becoming fertile; subiculum less than 1 mm. thick, concolorous with the margin, hyphae hyaline to yellowish under the microscope, apparently unbranched and aseptate, very thick-walled, 4–6 μ in diameter; tubes at length stratified, often oblique, the older layers white-stuffed, 2–6 mm. long each season; mouths circular to angular, 3–4 per mm., Cinnamon Buff to Clay Color; large crystalline bodies often abundant in the trama, hyphae of the trama yellowish under the microscope; basidia hyaline, 5–8 μ in diameter; spores hyaline, smooth, broadly ellipsoid, sometimes apiculate, 4–7 x 3–5 μ; no typical cystidia observed.

Habitat: on various coniferous hosts.

Distribution: foothill zone to subalpine zone. Widespread in the United States.

Occurrence: common. Summer and autumn.

Type of rot: white rot.

Compare with the preceding species, *Poria medulla-panis*.

62. Poria spissa (Schw.) Cooke, Grevillea **14:** 110. 1886.

Polyporus spissus Schw. in Fries, Elench. Fung. p. 111. 1828.

Polyporus salmonicolor Berk. & Curt. Hook. Jour. Bot. **1:** 104. 1849; Grevillea **1:** 53. 1872.

Polyporus laetificus Peck, Ann. Rept. N. Y. State Mus. **38:** 91. 1885.

Poria laetifica (Pk.) Sacc. Syll. Fung. **6:** 300. 1888.

Poria salmonicolor (Berk. & Curt.) Sacc. *ibid.* 318.

Plate 39, fig. 1.

Sporophores annual or perennial, inseparable to separable, 2–10 cm. broad, 3–50 cm. or more long, 1–6 mm. thick; subiculose margin arachnoid, tomentose, sterile to a breadth of 6 mm., at first whitish or yellowish, with age and on drying becoming as dark as Pecan Brown, hyphae of the margin yellowish-brown under the microscope, incrusted, 2–4 μ in diameter; subiculum less than 1 mm. thick, apparently absent in old specimens; tubes at length stratified, 0.5–1.5 mm. long each season, occasionally oblique; mouths circular to angular, 4–6 per mm., at first whitish to pale-salmon, with age and on bruising becoming reddish-brown, drying Orange-Cinnamon, Kaiser Brown, Bone Brown to Aniline Black; dissepiments entire, 30–50 μ thick, frequently containing large diamond-shaped crystals 12–15 μ broad and 30–40 μ long which may project beyond the level of the hymenium; spores smooth, hyaline, allantoid, 4–5 x 1–1.5 μ; no cystidia.

Habitat: on deciduous and coniferous hosts.

Distribution: montane and subalpine zones. Widespread in the United States.

Occurrence: rare. Autumn.

Type of rot: white rot.

The reddish color of the mouths and the sterile light-colored margin of this fungus are the outstanding characteristics. The color of young growing specimens is dilute red, which with age becomes darker. Dried specimens show a parallel variation in color from brownish-red to blackish-red, depending upon the age of the fungus when collected.

Only two collections of this species are known from Colorado; these were made by Kauffman at Tolland, Colorado, on the bark of pine and spruce.

63. Poria purpurea (Fr.) Cooke, Grevillea **14:** 112. 1886.
Polyporus purpurea Fries, Syst. Myc. **1:** 379. 1821.

Sporophores round, oblong, or effused for a distance of 30 cm. or more, inseparable, very thin, 0.5–2 mm.; margin at first white to yellowish, arachnoid, with age remaining sterile but changing to a reddish-purple color; subiculum very thin, 0.9–0.5 mm. thick, reddish-purple; tubes at first merulioid, with age becoming 0.5–2 mm. long; mouths circular to angular, unequal, averaging 3–5 per mm., at first yellowish in color, with age becoming brownish-purple to rose-purple, as: Purplish Vinaceous to Vinaceous Brown; hyphae of the trama slightly colored under the microscope, of varying diameters, 2–8 μ in diameter, thin-walled, incrusted; basidia hyaline, 3–6 μ in diameter; spores hyaline, smooth, allantoid 5–8 x 1.5–2.5 μ; no cystidia observed.

Habitat: on various deciduous hosts; probably also on conifers.

Distribution: montane and subalpine zones. Widespread in the United States.

Type of rot: white rot.

This fungus is characterized by its purplish color and allantoid spores. *Poria violacea*, which is reported to be extremely rare,[88] likewise is purplish in color, but differs from *P. purpurea* in having pores which average 2 per mm., and in having ovoid to ellipsoid spores measuring 5 x 2.5–3 μ.

64. Poria ferruginosa (Schrad.) Pers. Syn. Fung. p. 544. 1801.
Boletus ferruginosus Schrad. Spic. Fl. Germ. p. 172. 1794.
Polyporus ferruginosus (Schrad.) Fries, Syst. Myc. **1:** 378. 1821.
Polyporus Macouni Peck, Bot. Gaz. **4:** 169. 1879.
Fuscoporia ferruginosa (Schrad.) Murr. N. Am. Fl. **9:** 5. 1907.
Poria Macouni (Pk.) Overh. N. Y. State Mus. Rept. **71**^{2}**:** 86. 1917.

Plate 39, fig. 5.

Sporophores annual or perennial, woody, effused for a distance of 1 meter, 0.5–6 mm. thick, inseparable; subiculose margin entire to undulating, at first sterile to a breadth of 5 mm., tomentose, Ochraceous-Tawny, with age becoming fertile and thin or imbri-

[88] Murrill, W. A. Mycologia 13: 92. 1921.

cate-subpileate when growing on an irregular substratum; subiculum usually less than 1 mm. thick, Ochraceous-Tawny, hyphae apparently unbranched and aseptate, brownish under the microscope, 2–3 μ in diameter; tubes eventually stratified, often oblique, 1–6 mm. long each season, fulvous within; mouths circular to angular, averaging 4–6 per mm., Cinnamon, Sayal Brown to Snuff Brown; dissepiments entire, 40–80 μ thick; hymenium hyaline under the microscope, 8–12 μ broad; basidia hyaline, 4-spored, 4.5–6 μ in diameter; spores hyaline, smooth, ellipsoid, 4.5–5 x 2–3 μ; setae abundant, pointed, projecting 20–30(40) μ beyond the general level of the hymenium, 5–7 μ broad at their bases, similar in shape to those of *Trametes isabellina* (pl. 30, fig. 1).

Habitat: on various deciduous hosts; rare on conifers.

Distribution: foothill zone to subalpine zone. Widespread in the United States.

Occurrence: rare. Summer and Autumn.

Type of rot: white rot.

Poria ferruginosa may be differentiated from resupinate specimens of *Trametes isabellina* as follows: the spores of the former species are 4.5–5 x 2–3 μ and the setae project up to 30 μ; whereas the spores of the latter species are 6–9 x 2 μ and the setae project up to 50 μ.

This fungus is very common in eastern United States where deciduous trees predominate. However, in the Rocky Mountain region, where coniferous trees predominate, it is of rare occurrence.

Index to Species

Synonyms are printed in *italics*, previously published specific names in ordinary type, and genus names in CAPITALS. Pages on which genera and species are described are printed in **bold face** type.

abietina (Bull.) Fr. (Lenzites)..... 392
abietinella (Murr.) Sacc. & Trott. (Lenzites)..... 391
abietinellum Murr. (Gloeophyllum). 391
abietinus Dicks. (Boletus)..... 328
abietinus (Dicks.) Quél. (Coriolus) 328
abietinus (Dacryomyces)..... 292
abietinus (Dicks.) Fr. (Polyporus) 291, 292, 297, **328**, 331
abietinus (Dicks.) Sacc. & Cub. (Polystictus)..... 328
Abietis Karst. (Fomes)..... 379, 380
abietis Lloyd (Lenzites)..... 328
adusta (Willd.) Karst. (Bjerkandera) 339, 340
adustus Willd. (Boletus)..... 339
adustus (Willd.) Pk. (Myriadoporus) 339
adustus (Willd.) Fr. (Polyporus) 290, 291, 292, 306, **339**, 341
adustus crispus Pers. (Boletus)..... 340
Agassizii (Dasyscypha)..... 292
albidus Sow. (Boletus)..... 337
alboluteus (E. & E.) Murr. (Aurantiporellus)..... 333
alboluteus E. & E. (Fomes)..... 333
alboluteus E. & E. (Polyporus) 292, 304, 305, 307, 316, **333**, 335
alveolaris (DC.) Fr. (Cantharellus). 394
alveolaris (DC.) Quél. (Favolus)..347, **394**
alveolaris (DC.) Murr. (Hexagona). 394
alveolaris DC. (Merulius)..... 394
anceps Pk. (Polyporus)..... **343**
anceps (Pk.) Murr. (Tyromyces)... 343
annosa (Fr.) Karst. (Fomitopsis)... 389
annosa (Fr.) Pat. (Ungulina)..... 389
annosum (Fr.) Bref. (Heterobasidion)..... 389
annosus (Fr.) Cooke (Fomes)..... **389**
annosus Fr. (Polyporus)..... 389
applanata (Pers.) Karst. (Elfvingia) 374
applanatum (Pers.) Pat. (Ganoderma)..... **374**
applanatus Pers. (Boletus)..... 374
applanatus (Pers.) Gill. (Fomes)... 374
applanatus (Pers.) Schroet. (Phaeoporus)..... 374
applanatus (Pers.) Quél. (Placodes). 374
applanatus (Pers.) Wallr. (Polyporus)..... 374
arida (Dasyscypha)..... 292
arculariformis Murr. (Polyporus)... 346
arcularius Batsch (Boletus)....346, 394
arcularius Schw. (Boletus).....346, 394
arcularius (Batsch) Fr. (Polyporus) **346**, 395
aurantiacus Pk. (Polyporus)..... 334
auricula-Judae (Auricularia)..... 292
azureus Fr. (Polystictus)..... 323
benzoina (Wahlenb.) Fr. (Trametes) 338
benzoinus Wahlenb. (Boletus)..... 338
benzoinus (Wahlenb.) Fr. (Polyporus)..... 338
boletiformis Sow. (Agaricus)..... 391
borealis Fr. (Polyporus)..... **335**
borealis (Fr.) Pat. (Spongipellis)... 335
Boucheanus peponinus B. & C. (Polyporus)..... 394
caesius Schrad. (Boletus)..... 337
caesius (Schrad.) Fr. (Polyporus).. **337**
caesius (Schrad.) Murr. (Tyromyces) 337
calceolus Bull. (Boletus)..... 358
calceolus (Bull.) Murr. (Polyporus). 358
callosa (Fr.) Sacc. (Poria).....365, 396
callosus Fr. (Polyporus)..... 365
canadensis Klotz. (Favolus)....394, 395
carnea Cooke (Trametes)..... 372
carpineus Sow. (Boletus)..... 339
caudicinus Murr. (Polyporus)..... 356
Celottianus S. & M. (Polystictus).. 368
cervinus Pers. (Polyporus)..... 367
cinnabarina (Jacq.) Fr. (Trametes). 342
cinnabarinus Jacq. (Boletus)..... 342
cinnabarinus (Jacq.) Fr. (Polyporus) 334, **342**
cinnabarinus (Jacq.) Sacc. (Polystictus)..... 342

cinnabarinus (Jacq.) Karst. (Pycnoporus) 342
cinnamomea (Jacq.) Murr. (Coltricia) 354
cinnamomea Gray (Strilia) 354
cinnamomeus Jacq. (Boletus) 354
cinnamomeus (Jacq.) Fr. (Polyporus) **354**
cinnamomeus (Jacq.) Sacc. (Polystictus) 354
circinatus Fr. (Polyporus) **349**
circumstans Morg. (Polyporus) 388
coccineus Bull. (Boletus) 342
columnaris (Calyptospora) 293
conchatus Pers. (Boletus) 384
conchatus (Pers.) Gill. (Fomes) . . . 316, 368, 381, **384**
conchatus (Pers.) Fr. (Polyporus) . . . 384
conchatus (Pers.) Murr. (Pyropolyporus) 384
confluens Schum. (Boletus) 352, 353
confluens A. & S. (Boletus) 352, 353
confluens (A. & S.) Fr. (Polyporus) **351**
connata Gray (Coltricia) 353
contigua (Pers.) Fr. (Poria) 364
coriaceus Scop. (Boletus) 353
corruscans Fr. (Polyporus) 336
crispus Pers. (Boletus) 340
crispus (Pers.) Fr. (Polyporus) **340**
cryptopus E. & B. (Polyporus) **355**
cryptopus (E. & B.) Murr. (Scutiger) 355
CYCLOMYCES Kunz. & Fr. 314
DAEDALEA (Pers.) Fr. 314, 376
Demidoffii (Lév.) Sacc. & Syd. (Fomes) **385**, 388
Demidoffii Lév. (Polyporus) 385
dryophilus (Berk.) Murr. (Inonotus) 336
dryophilus Berk. (Polyporus) 336
dualis Pk. (Polyporus) 349
Earlei (Murr.) Sacc. & Sacc. (Fomes) 385, 386
Earlei Murr. (Pyropolyporus) 385
elegans Bull. (Boletus) 359
elegans (Bull.) Fr. (Polyporus) **359**
Ellisianus And. (Fomes) 388
Ellisianus (Murr.) Sacc. & Trott. (Polyporus) 343
Ellisianus Murr. (Tyromyces) 343
epigaea Lenz (Daedalea) 347
europaeus Fr. (Favolus) 394, 395
FAVOLUS Beauv. 313, 317, **394**
Fergussoni Cooke (Polystictus) 368
ferruginosa (Schrad.) Murr. (Fuscoporia) 401
ferruginosa (Schrad.) Pers. (Poria). 364, **401**
ferruginosus Schrad. (Boletus) 401
ferruginosus (Schrad.) Fr. (Polyporus) 401
fibrillosus Karst. (Inonotus) 334
fibrillosus Karst. (Polyporus) . . . 316, **334**
fibrillosus (Karst.) Murr. (Pycnoporellus) 334
Flabellum Mont. (Polyporus) 329
FOMES (Fr.) Gill. . . 313, 317, 362, **376**, 396
fragilis Fr. (Polyporus) 333, **341**
fragilis (Fr.) Murr. (Spongipellis) . . 341
fraxinophilus (Pk.) Sacc. (Fomes) . . 389
fraxinophilus f. Ellisianus (And.) Baxter (Fomes) **388**
fuliginosa (Scop.) Pat. (Ungulina) . . 338
fuliginosum (Scop.) Murr. (Ischnoderma) 338
fuliginosus Scop. (Boletus) 338
fuliginosus (Scop.) Sacc. (Fomes) . . 338
fuliginosus (Scop.) Fr. (Polyporus). 338
fulvus Schaeff. (Boletus) 377, 383
fulvus Scop. (Boletus) 377, 383
fulvus (Scop.) Gill. (Fomes) **383**, 385
fulvus (Scop.) Quél. (Placodes) 383
fulvus (Scop.) Fr. (Polyporus) 383
fulvus (Scop.) Murr. (Pyropolyporus) 383
fuscoporus Planer (Boletus) 339
gallica Fr. (Trametes) 369
GANODERMA (Karst.) Pat. 313, 314, **373**, 376
Gillotii Roum. (Polyporus) 389
glandulosa (Exidia) 292
grossus Kalchbr. (Irpex) 368
heteromorpha Fr. (Daedalea) 366
heteromorpha Fr. (Lenzites) 366
heteromorpha (Fr.) Lloyd (Trametes) 365, **366**
HEXAGONA Fr. 394
hexagoniformis Murr. (Coriolus) . . . 366
hirsuta (Schaeff.) Murr. (Sesia) 391
hirsutulus (Schw.) Murr. (Coriolus) 323
hirsutulus Schw. (Polyporus) 323

hirsutum (Schaeff.) Murr. (Gloeophyllum) ... 370, 391
hirsutus Schaeff. (Agaricus) ... 391
hirsutus Wulf. (Boletus) ... 324
hirsutus (Wulf.) Fr. (Polyporus) ... **324**, 326, 340
hirsutus (Wulf.) Sacc. (Polystictus) 324
hirtellus Fr. (Polystictus) ... 324
hirtus Quél. (Polyporus) ... 357
hispida Pass. (Trametes) ... 290, 291, 306, **368**
hispidellus Pk. (Polyporus) ... 357
hispidellus (Pk.) Murr. (Scutiger) .. 357
hispidoides Pk. (Polyporus) ... 347, 348
hyperboreus Berk. (Polyporus) ... 382
igniarius L. (Boletus) ... 382
igniarius (L.) Gill. (Fomes) ... 292, **382**. 384, 385
igniarius (L.) Quél. (Phellinus) ... 382
igniarius (L.) Fr. (Polyporus) ... 382
ilicincola B. & C. (Polyporus) ... 330
incarnatus Schum. (Boletus) ... 328
incerta (Pers.) Murr. (Poria) ... 397
incertus Pers. (Boletus) ... 397
inflatus E. & M. (Polyporus) ... 321
IRPEX Fr. ... 334
irregularis Underw. (Polyporus) ... 389
isabellina Fr. (Trametes) .. 292, **363**, 380
isabellinus Schw. (Boletus) ... 339
isabellinus (Fr.) B. & G. (Phellinus) 363
Juniperinus (von Schrenk) Sass. & Syd. (Fomes) ... 385, 386
Juniperinus (von Schrenk) Murr. (Fulvifomes) ... 385
Juniperinus von Schrenk (Polyporus) ... 385
Juniperinus (von Schrenk) Murr. (Pyropolyporus) ... 385
laceratus Berk. (Polyporus) ... 329
laceratus Lloyd (Trametes) ... 366
laeticolor Murr. (Scutiger) ... 352
laetifica (Pk.) Sacc. (Poria) ... 400
laetificus Pk. (Polyporus) ... 400
LENZITES Fr. ... 313, 376, **390**
leucomelas (Pers.) Fr. (Polyporus). 288
leucophaeum (Mont.) Pat. (Ganoderma) ... 374
leucophaeus (Mont.) Cooke (Fomes) 374, 376
leucophaeus Mont. (Polyporus) ... **374**
leucospongia C. & H. (Polyporus) .. 292, 299, 304, 305, 307, 308, **326**
leucospongia (C. & H.) Murr. (Spongiporus) ... 326
Lindheimeri B. & C. (Polyporus) ... 368
lipsiensis Bat. (Boletus) ... 374
lipsiensis (Bat.) Murr. (Elfvingia) .. 374
lipsiensis (Bat.) Atk. (Ganoderma) 374
Lloydii Murr. (Coriolus) ... 326
Lloydii (Murr.) Overh. (Polyporus). 326
loricatus Pers. (Polyporus) ... 384
Macouni Pk. (Polyporus) ... 401
Macouni (Pk.) Overh. (Poria) ... 401
marginata (Pers.) Pat. (Ungulina) .. 377
marginatus Pers. (Boletus) ... 377
marginatus (Pers.) Gill. (Fomes) ... 377
marginatus (Pers.) Fr. (Polyporus). 377
medulla-panis Jacq. (Boletus) ... 398
medulla-panis (Jacq.) Fr. (Polyporus) ... 398
medulla-panis (Jacq.) Pers. (Poria) **398**
megaloma (Lév.) Murr. (Elfvingia) .. 374
megaloma (Lév.) Cooke (Fomes) ... 374
megaloma Lév. (Polyporus) ... 374
Menandianus Mont. (Polyporus) ... 329
MERULIUS Fr ... 322
micropora Murr. (Hexagona) ... 394
mollis (Sommerf.) Karst. (Antrodia) 367
mollis Sommerf. (Daedalea) ... 367
mollis (Fr.) Pers. (Polyporus) ... 342
mollis (Sommerf.) Fr. (Trametes) .. 367
monticola (Guepinia) ... 292
monticola Murr. (Poria) ... **396**
Mori Polli. (Hexagona) ... 394
mucida Pers. (Poria) ... 398
nigrella (Paxina) ... 293
nigricans (Fr.) Gill. (Fomes) ... 382
nigricans Fr. (Polyporus) ... 382
nigrolimitatus (Rom.) Egel. (Fomes) 316, 364, 368, **380**, 385
nigrolimitatus (Rom.) B. & G. (Phellinus) ... 380
nigrolimitatus Rom. (Polyporus) ... 380
nigromarginatus Schw. (Boletus) ... 324
nigromarginatus (Schw.) Murr. (Coriolus) ... 324
Novae-Angliae B. & C. (Polyporus) 382
nummularis Bull. (Boletus) ... 359

oblectans Berk. (Polyporus)........ 354
obvolutus Berk. & Cooke (Polyporus) 321
occidentalis Murr. (Spongipellus)... 345
odorata (Wulf.) Fr. (Trametes)....
291, 292, 308, **370**, 392
odoratus Wulf. (Boletus)........... 370
odoratus (Wulf.) Schroet. (Ochroporus)........................ 370
odoratus (Wulf.) Fr. (Polyporus)... 370
ohiensis B. & M. (Favolus)........ 394
ohiensis (Berk.) Murr. (Fomes).... 376
osseus Kalchb. (Polyporus)........
316, **360**, 368
ovinus Schaeff. (Boletus).......... 350
ovinus (Schaeff) Fr. (Polyporus)...
316, **350**, 368
ovinus (Schaeff.) Murr. (Scutiger)... 350
pallescens Fr. (Polyporus)......... 339
pallidofulva Murr. (Sesia)......... 393
pallidofulvum Murr. (Gloeophyllum) 393
pargamenus (Fr.) Pat. (Coriolus)... 330
pargamenus Fr. (Polyporus)... **329**, 332
pargamenus (Fr.) Sacc. (Polystictus) 330
parvulus Schw. (Polyporus).....328, 354
parvulus Klotz. (Polyporus)....... 354
Peakensis Lloyd (Polyporus)...349, 350
Peckii Kalchbr. (Trametes)....368, 370
pelleporus Bull. (Boletus)......... 339
perennis L. (Boletus)............. 353
perennis (L.) Murr. (Coltricia)..... 353
perennis (L.) Quél. (Pelloporus).... 353
perennis (L.) Fr. (Polyporus)...**353**, 355
perennis (L.) Karst. (Polystictus).. 353
pergamenus (Fr.) Sacc. (Polystictus) 330
piceinus Pk. (Polyporus).......379, 380
piceinus (Pk.) Sacc. (Polystictus)...
379, 380
picipes Fr. (Polyporus)........... 359
Pini Thore (Boletus)............. 379
Pini (Thore) Fr. (Daedalea)...... 379
Pini (Thore) Lloyd (Fomes).......
291, 292, 297, 307, 308, 364, **379**
Pini (Thore) Pers. (Polyporus).... 379
Pini (Thore) Murr. (Porodaedalea) 379
Pini (Thore) Fr. (Trametes)...379, 380
Pini Abietis Karst. (Trametes).379, 380
pinicola Sw. (Boletus)............ 377
pinicola (Sw.) Cooke (Fomes).....
291, 292, 307, 308, 316, **377**
pinicola (Sw.) Karst. (Fomitopsis).. 377
pinicola (Sw.) Fr. (Polyporus)..... 377
planellus Murr. (Coriolus)......... 344
planellus (Murr.) Overh. (Polyporus)......................... **344**
planus Pk. (Polyporus)........... 344
POLYPORUS (Mich.) Fr. 313, **317**, 362, 396
POLYSTICTUS Fr.................. 313
pomaceus Pers. (Boletus).......... 383
pomaceus (Pers.) B. & G. (Fomes).. 383
pomaceus (Pers.) Quél. (Placodes).. 383
pomaceus Pers. (Polyporus)....... 383
ponderosus von Schrenk (Fomes)... 378
PORIA Pers...................313, **395**
prolificans (Fr.) Murr. (Coriolus)... 330
prolificans Fr. (Polyporus)........ 329
protracta Fr. (Trametes)..........
291, 370, 371, 392
pseudopargamenus Thuem. (Polyporus)....................... 330
pubescens (Schum.) Fr. (Polyporus) 326
purpurea Fr. (Polyporus)......... 401
purpurea (Fr.) Cooke (Poria)...... **401**
pusio Sacc. & Cub. (Polystictus)... 328
putearius Weir (Fomes)........... 381
radiciperda Hartig (Trametes)..... 389
resinosum (Schrad.) Karst. (Ischnoderma)...................... 338
resinosus Schrad. (Boletus)........ 338
resinosus Rostk. (Polyporus)...338, 389
resinosus (Schrad.) Fr. (Polyporus)
338, 389
rhabarbarina B. & C. (Lenzites).... 391
Rheades Pers. (Boletus)........... 336
Rheades (Pers.) Fr. (Polyporus)... **336**
rosea (A. & S.) Karst. (Fomitopsis). 387
rosea (A. & S.) Pat. (Ungulina).... 387
roseus A. & S. (Boletus).......... 387
roseus (A. & S.) Cooke (Fomes)....
372, **387**
roseus (A. & S.) Fr. (Polyporus)... 387
rufo-pallidus Trog (Polyporus)..... 387
rugisporum (Stereum)............ 292
saepiaria (Wulf.) Fr. (Daedalea)... 391
saepiaria (Wulf.) Fr. (Lenzites) .291, 292,
293, 297, 300, 305, 307, 371, **391**, 393
saepiaria porosa Pk. (Lenzites).... 370
saepiarius Wulf. (Agaricus)....... 391
salicinus Bull. (Boletus).......... 384

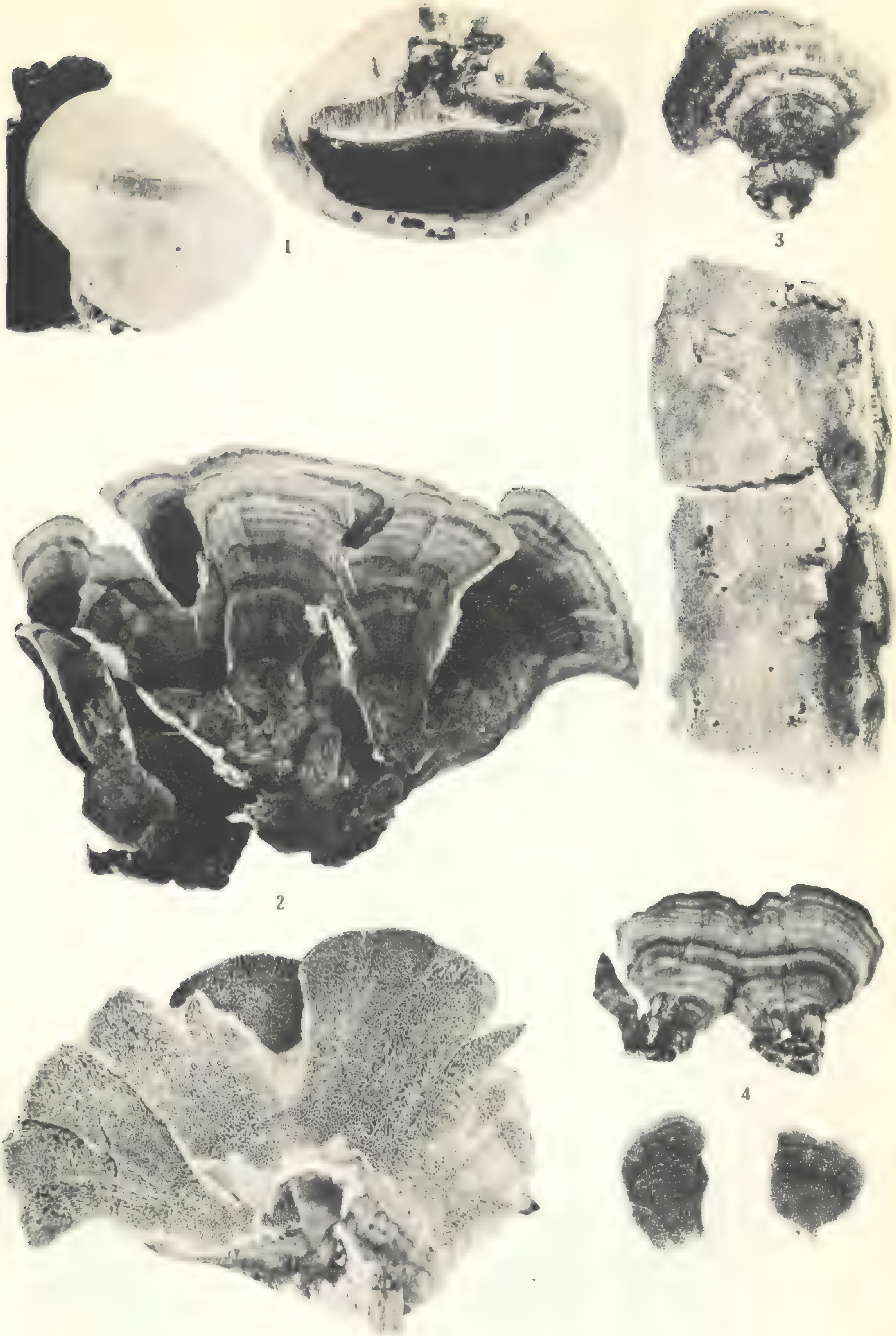
salicinus Pers. (Boletus).......... 384
salicinus (Pers.) Quél. (Phellinus).. 384
salicinus (Pers.) Fr. (Polyporus)... 384
salmonicolor B. & C. (Polyporus)... 400
salmonicolor (B. & C.) Sacc. (Poria) 400
Sartwellii B. & C. (Polyporus)..... 330
scalaris Pers. (Polyporus)......... 365
Schweinitzii (Fr.) Quél. (Cladomeris) 347
Schweinitzii Fr. (Polyporus)....... **347**
Schweinitzii (Fr.) Karst. (Polystictus).......................... 347
scuirinus Kalchbr. (Polystictus).... 368
scutellatus (Schw.) Cooke (Fomes). 376
semiovatus Schaeff. (Boletus)...... 377
Sepium (Berk.) Murr. (Coriolellus) 366
serialis (Fr.) Murr. (Coriolellus)... 365
serialis Fr. (Polyporus)........... 365
serialis Fr. (Trametes)....297, **365**, 396
serpens Fr. (Lenzites)............. 315
serpentarius Pers. (Polyporus)..... 389
setosus Weir (Trametes).......... 363
Shiraianus Henn. (Polyporus)..... 334
sistotremoides A. & S. (Boletus).... 347
sistotremoides (A. & S.) Murr. (Phaeolis).......................... 347
spectabilis Fr. (Polyporus)......... 347
spissa (Schw.) Cooke (Poria)....... **400**
spissus Schw. (Polyporus)......... 400
splendens Pk. (Polyporus)......... 354
spumeus Sow. (Boletus)........... 345
spumeus (Sow.) Fr. (Polyporus)... **345**
spumeus (Sow.) Pat. (Spongipellus) 345
squamosus Huds. (Boletus)........ 356
squamosus (Huds.) Fr. (Polyporus) **356**
stereoides Fr. (Polyporus)......... 367
stereoides (Fr.) Bres. (Trametes)... 316, **367**
striatula (E. & E.) Murr. (Hexagona).......................... 394
striatulus E. & E. (Favolus)....... 394
stuppea (Berk.) Murr. (Funalia)... 368
stuppeus Berk. (Trametes)........ 370
subacida Pk. (Polyporus).......... 399
subacida (Pk.) Sacc. (Poria)....... **399**
subchartaceus Murr. (Coriolus)..... 331
subchartaceus (Murr.) Overh. (Polyporus)....................329, **331**
subchartaceus (Murr.) Sacc. & Trott. (Polystictus).................. 331
subcinereus Berk. (Polyporus)..... 339
suberosus flabelliformis Bat. (Boletus)........................ 339
subflavus Lév. (Polyporus)........ 330
subpileatus Weinm. (Polyporus).... 389
subrosea Weir (Trametes)......... 291, 308, **372**, 388
subsericeus Pk. (Polyporus)........ 354
subsquamosus (L.) Fr. (Polyporus) 351
subtomentosus Bolt. (Boletus)...... 353
superficialis (Schw.) Cooke (Poria). 364
tabulaeformis Berk. (Polyporus). 347, 348
tenuis Karst. (Fomes)............ 363
tenuis (Karst.) Rom. (Polyporus).. 363
tenuis (Karst.) (Trametes)........ 363
tomentosa (Fr.) Murr. (Coltricia)... 349
tomentosus Fr. (Polyporus).....349, 350
trabea (Pers.) Fr. (Daedalea)...... 392
trabea (Pers.) Fr. (Lenzites)...371, **392**
trabeum (Pers.) Murr. (Gloeophyllum)........................ 393
trabeus Pers. (Agaricus)........... 392
TRAMETES Fr.....313, 317, **362**, 376, 396
ungulatus Schaeff. (Boletus)....... 377
ungulatus (Schaeff.) Sacc. (Fomes). 377
unicolor violacea Clem. (Daedalea).. 328
ursinus Lloyd (Polyporus)......... 292, 308, **332**, 342
Vaillantii Fr. (Poria)............. 398
vaporaria Fr. (Polyporus)......... 397
vaporaria (Fr.) Cooke (Poria)...... **397**
vaporaria Pers. (Poria)........... 397
variiformis Pk. (Polyporus)........ 365
variiformis Pk. (Trametes). 292, **365**, 367
varius Pers. (Boletus)............. 358
varius (Pers.) Fr. (Polyporus)..**358**, 360
versicolor L. (Boletus)............. 323
versicolor (L.) Quél. (Coriolus)..... 323
versicolor (L.) Fr. (Polyporus)...... 290, 291, 306, **323**, 345
versicolor (L.) Sacc. (Polystictus)... 323
vialis Pk. (Lenzites).............. 392
violacea (Fr.) Bres. (Poria)........ 401
viticola (Schw.) Cooke (Poria)..... 364
volvata (Pk.) Pat. (Ungulina)...... 321
volvata var. *pleurostoma* (Pk.) Pat. (Ungulina).................. 321
volvatus (Pk.) Shear (Cryptoporus). 321
volvatus Pk. (Polyporus)......291, **321**

volvatus Helix Henn. (Polyporus)... 321
Whiteae Murr. (Scutiger).......... 352
xalapensis B. & C. (Polyporus).... 330
xantholoma Schw. (Polyporus)..... 398
xantholoma (Schw.) Cooke (Poria).. 398
Zelleri Murr. (Polyporus)......360, 361
zonatus (Fr.) Quél. (Coriolus)...... 325
zonatus Fr. (Polyporus).......324, **325**
zonatus (Fr.) Sacc. (Polystictus)... 326

Explanation of Plate

PLATE 16

Fig. 1. *Polyporus volvatus* Pk. × 1. Habit and section views.
Fig. 2. *Polyporus versicolor* (L.) Fr. × 1. Upper and lower surfaces.
Fig. 3. *Polyporus zonatus* Fr. × 1. Upper and lower surfaces.
Fig. 4. *Polyporus pargamenus* Fr. × 1. Upper and lower surfaces.



SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

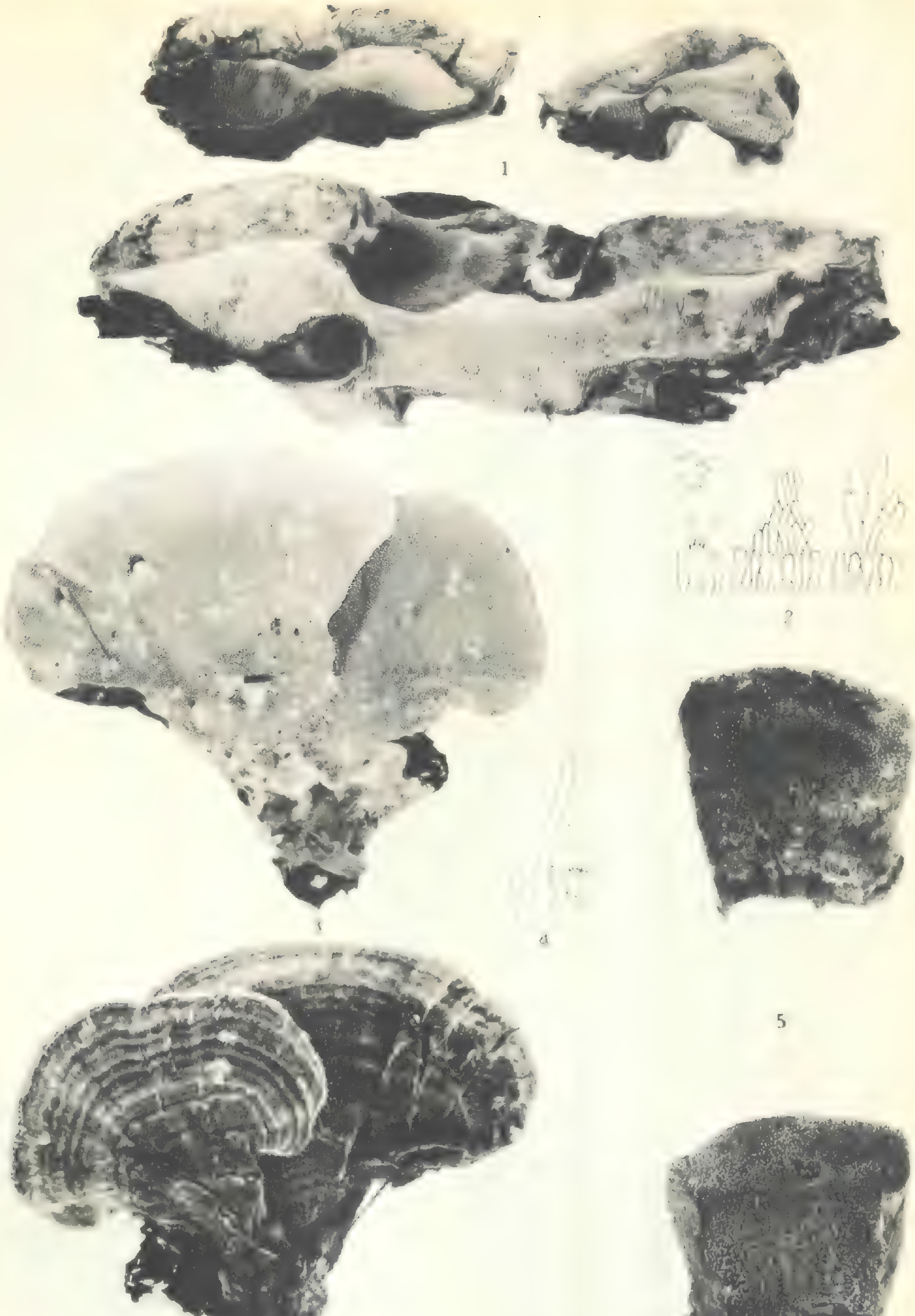
Explanation of Plate

PLATE 17

Figs. 1–2. *Polyporus leucospongia* Cooke & Hark. Fig. 1 shows three sporophores × 1. Fig. 2 shows a basidium, spores, and hyphal pegs. × 450.

Fig. 3. *Polyporus hirsutus* (Wulf.) Fr. × 1. Upper and lower surfaces.

Figs. 4–5. *Polyporus fibrillosus* Karst. Fig. 4 shows a basidium, spores, and a cystidium. × 450. Fig. 5 shows the upper and lower surfaces. × 1.



SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 18

Fig. 1. *Polyporus subchartaceus* (Murr.) Overh. × 1. Habit, pore layer, and section views.

Figs. 2–6. *Polyporus abietinus* (Dicks.) Fr. The poroid and lamellate hymenia are shown in figs. 2 and 3 respectively; fig. 4 shows a vertical section, and fig. 6 a habit view. × 1. Fig. 5 shows a basidium, spores, and incrusted and smooth cystidia. × 450.

SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 19

Figs. 1–4. *Polyporus alboluteus* Ell. & Ev. Figs. 1–3 show section views and front view. × 1. Fig. 4 shows a cystidium and spores. × 450.

Figs. 5–8. *Polyporus ursinus* Lloyd. Figs. 5 and 6 show saturated and air-dry halves of a single sporophore; fig. 7 shows upper and lower surfaces. × 1. Fig. 8 shows basidia, spores, and incrusted cystidia. × 450.

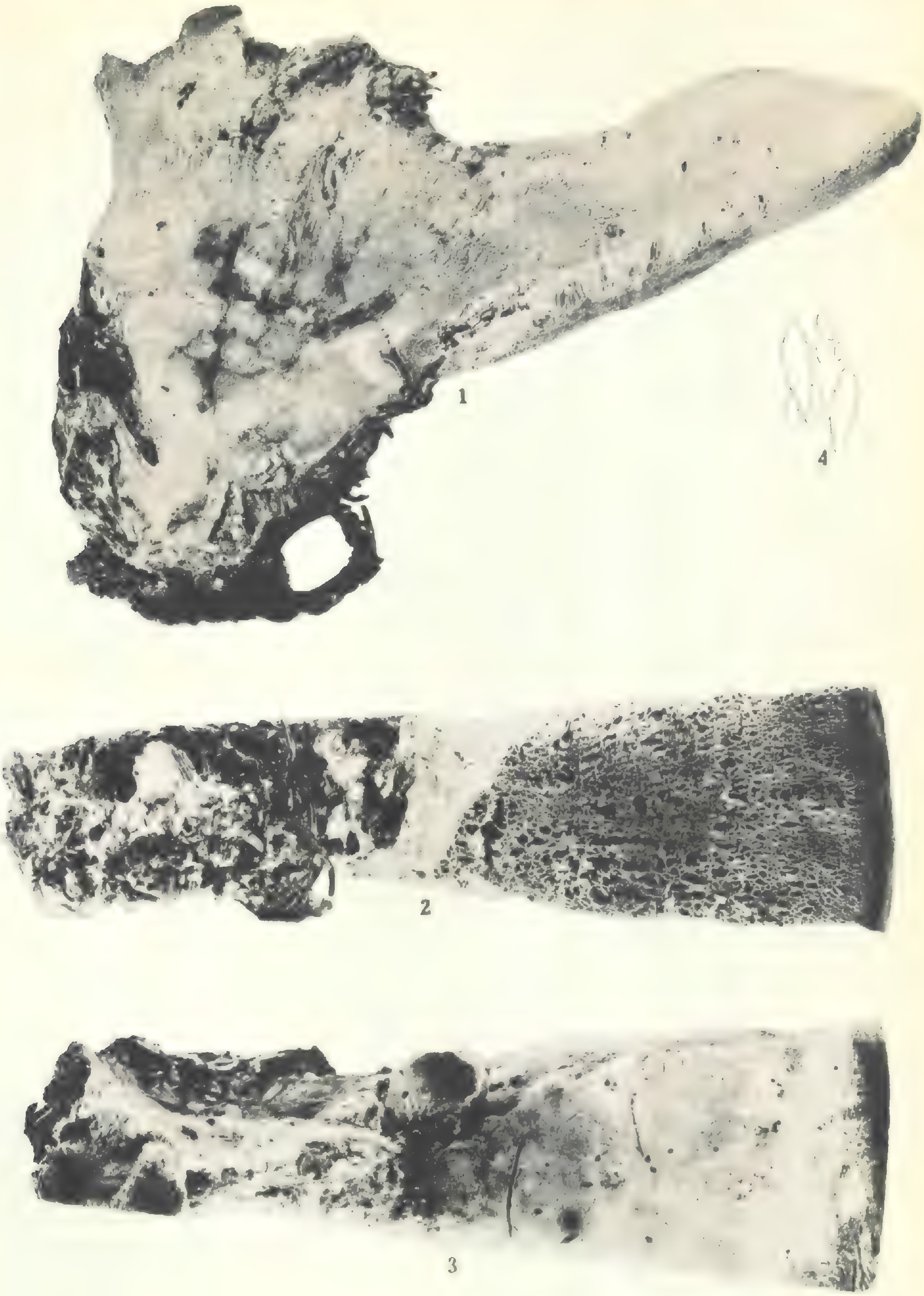
SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 20

Figs. 1–4. *Polyporus borealis* Fr. Figs. 1–3 show vertical section, pore layer, and upper surface. × 1. Fig. 4 shows spores and cystidia. × 450.



SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 21

Figs. 1–4. *Polyporus adustus* (Willd.) Fr. × 1. Figs. 1 and 3 show the pore layers of young and old sporophores; fig. 2 habit view, and fig. 4 vertical sections.

Figs. 5–6. *Polyporus Rheades* (Pers.) Fr. × 1. Fig. 5 shows small aspen form; fig. 6 shows large oak form with a large central core.

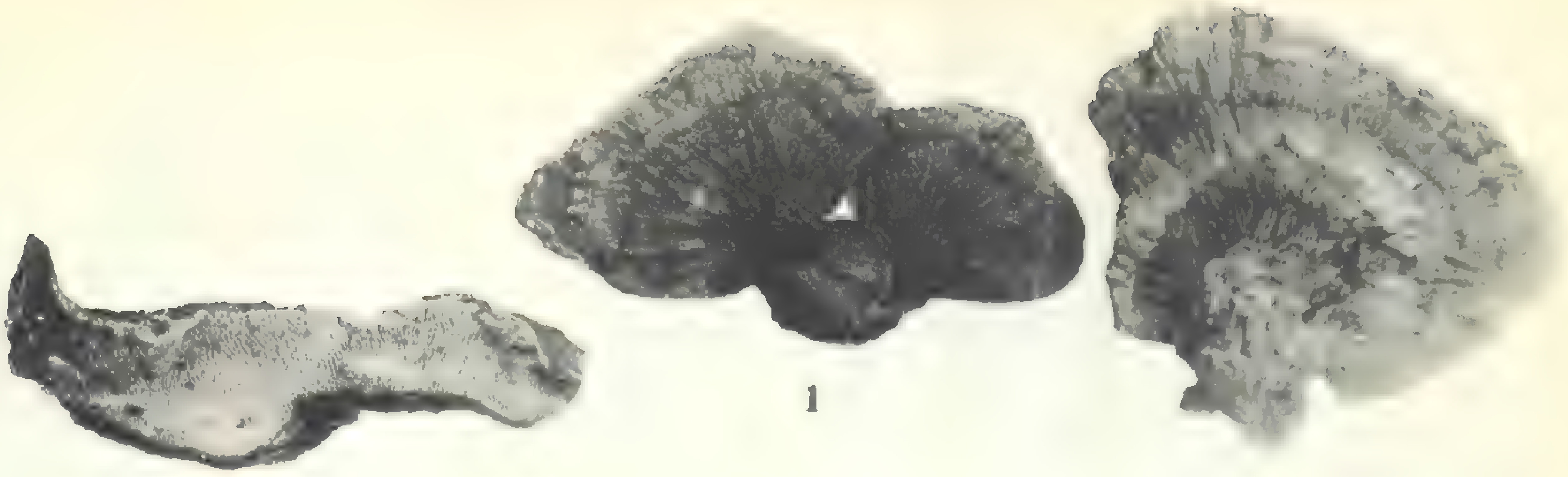
SHOPE — POLYPORACEAE OF COLORADO

Explanation of Plate

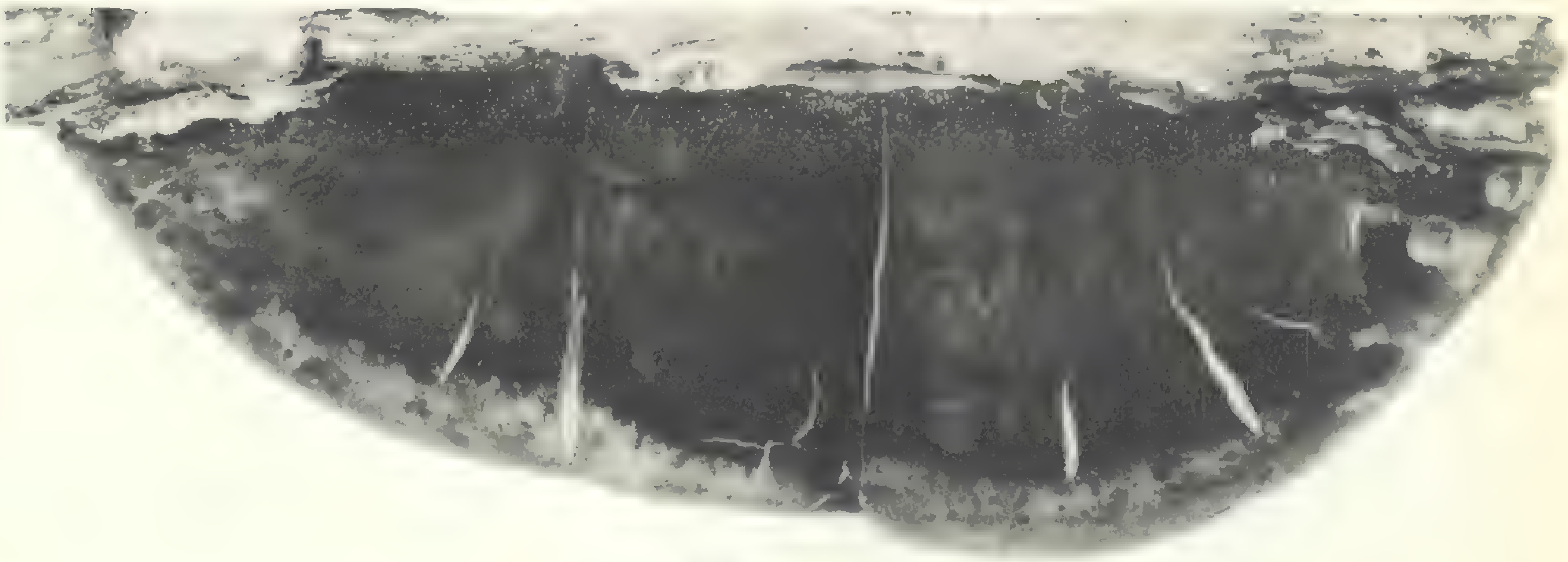
PLATE 22

Fig. 1. *Polyporus planellus* (Murr.) Overh. × 1. Three sporophores showing upper and lower surfaces.

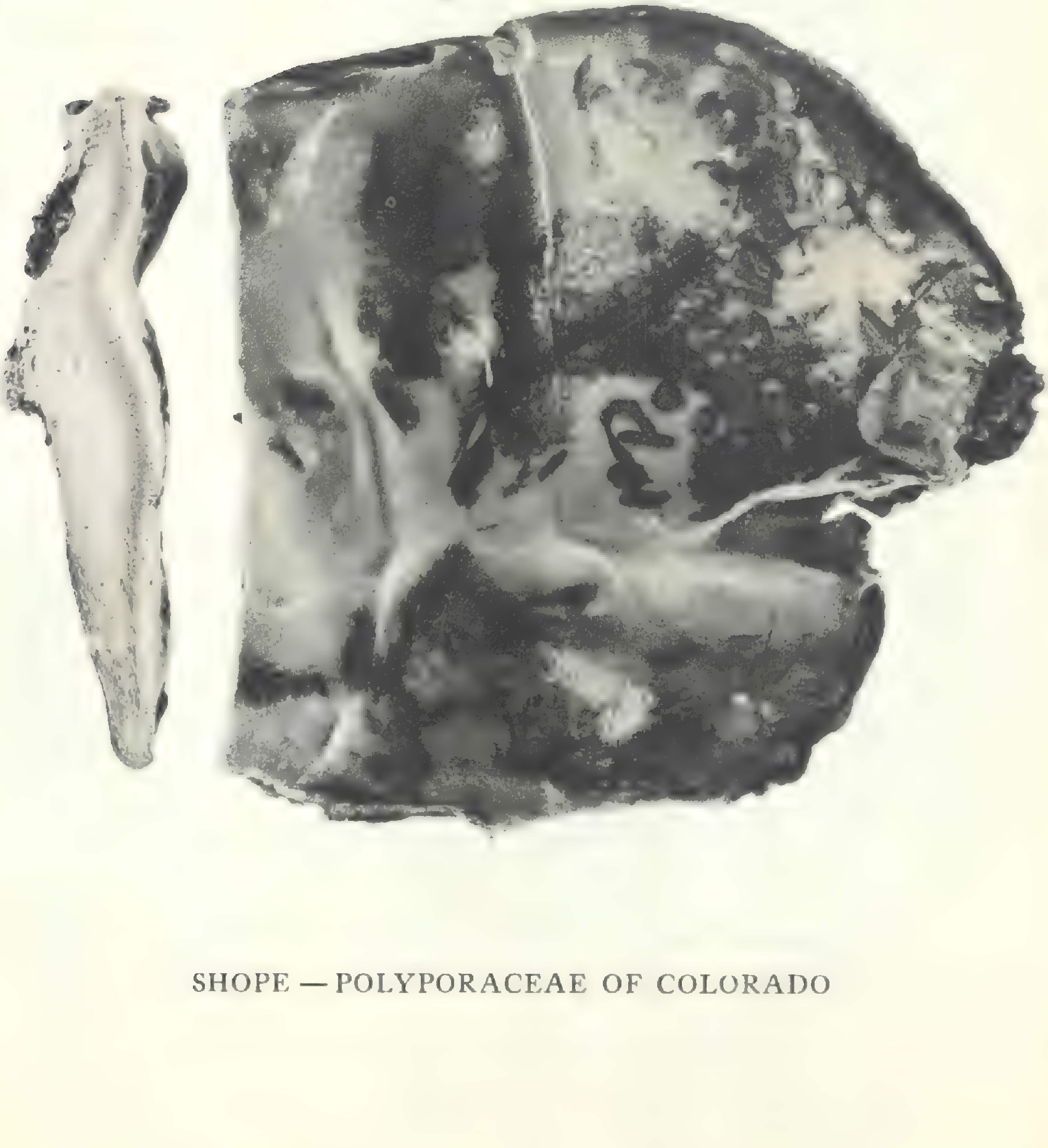
Fig. 2. *Polyporus resinosus* (Schrad.) Fr. × 1. Upper and lower surfaces and vertical section are shown.



1



2



SHOPE — POLYPORACEAE OF COLORADO

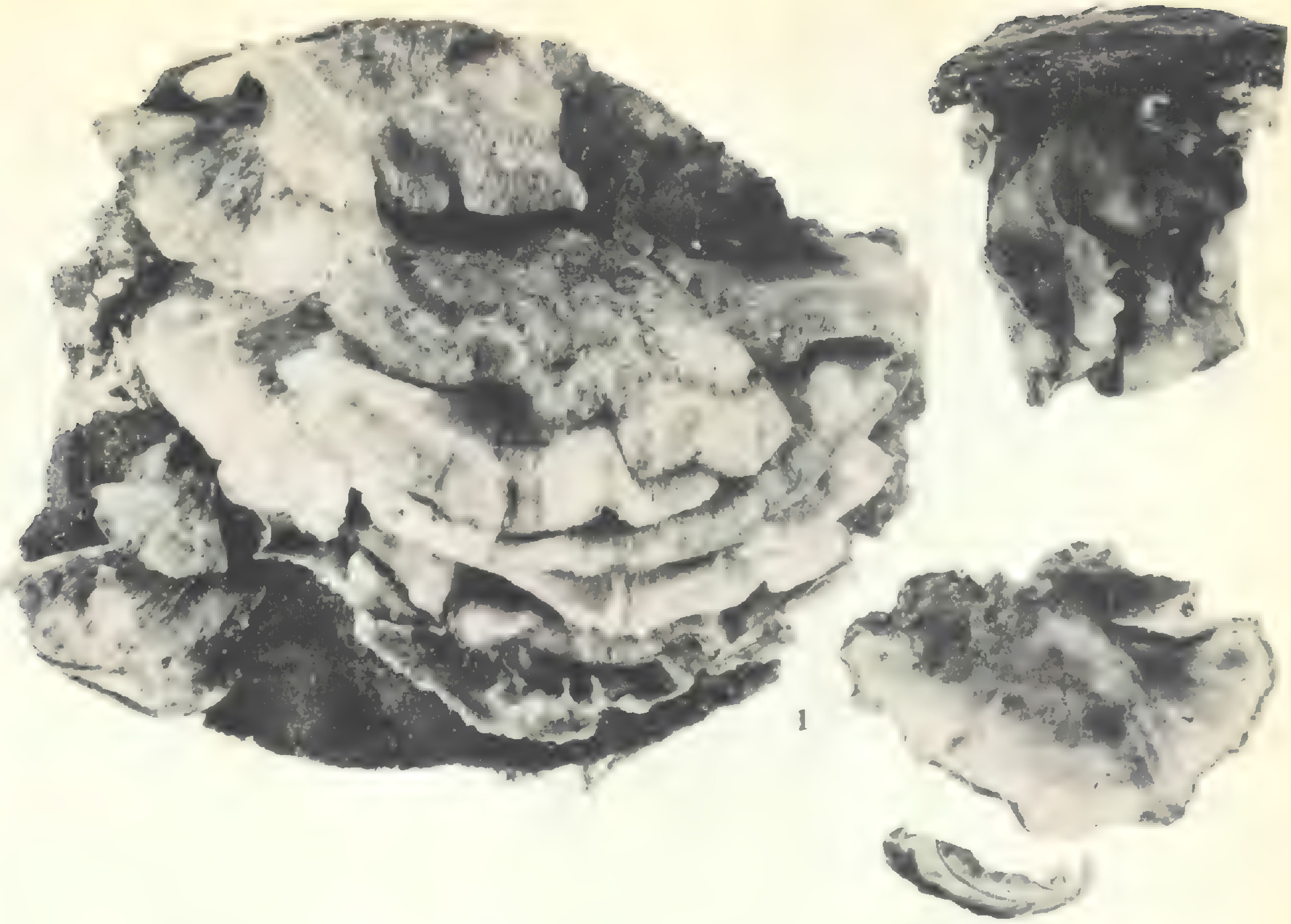
COCKAYNE, BOSTON

Explanation of Plate

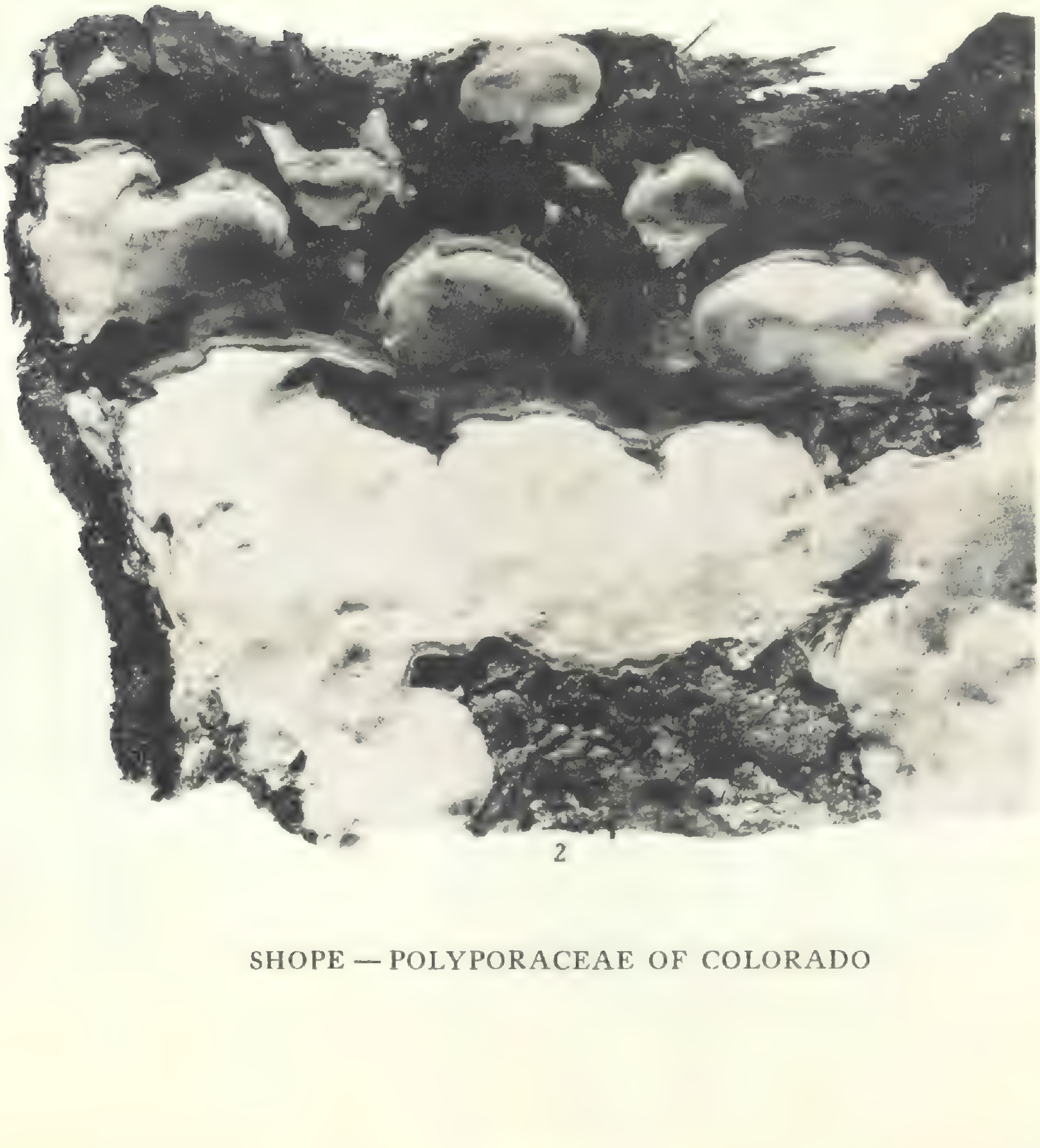
PLATE 23

Fig. 1. *Polyporus crispus* (Pers.) Fr. × 1. The imbricate growth-form is shown in the upper left photograph; to the right are shown the pore layer and section views.

Fig. 2. *Polyporus anceps* Pk. × 1. Habit view.



1



2

SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 24

Fig. 1. *Polyporus cinnabarinus* (Jacq.) Fr. × 1. Upper and lower surfaces.

Fig. 2. *Polyporus ovinus* (Schaeff.) Fr. × 1. Photograph by C. G. Lloyd, courtesy of the Smithsonian Institution.

Fig. 3. Three views of *Polyporus cinnamomeus* (Jacq.) Fr. × 1.

Fig. 4. *Polyporus fragilis* Fr. × 1. Upper surface.

Figs. 5–6. *Polyporus arcularius* (Batsch) Fr. Fig. 5 shows habit view. × 1. Fig. 6 shows gelatinized hyphal peg in which the individual hyphae are scarcely discernible. × 450.

SHOPE — POLYPORACEAE OF COLORADO

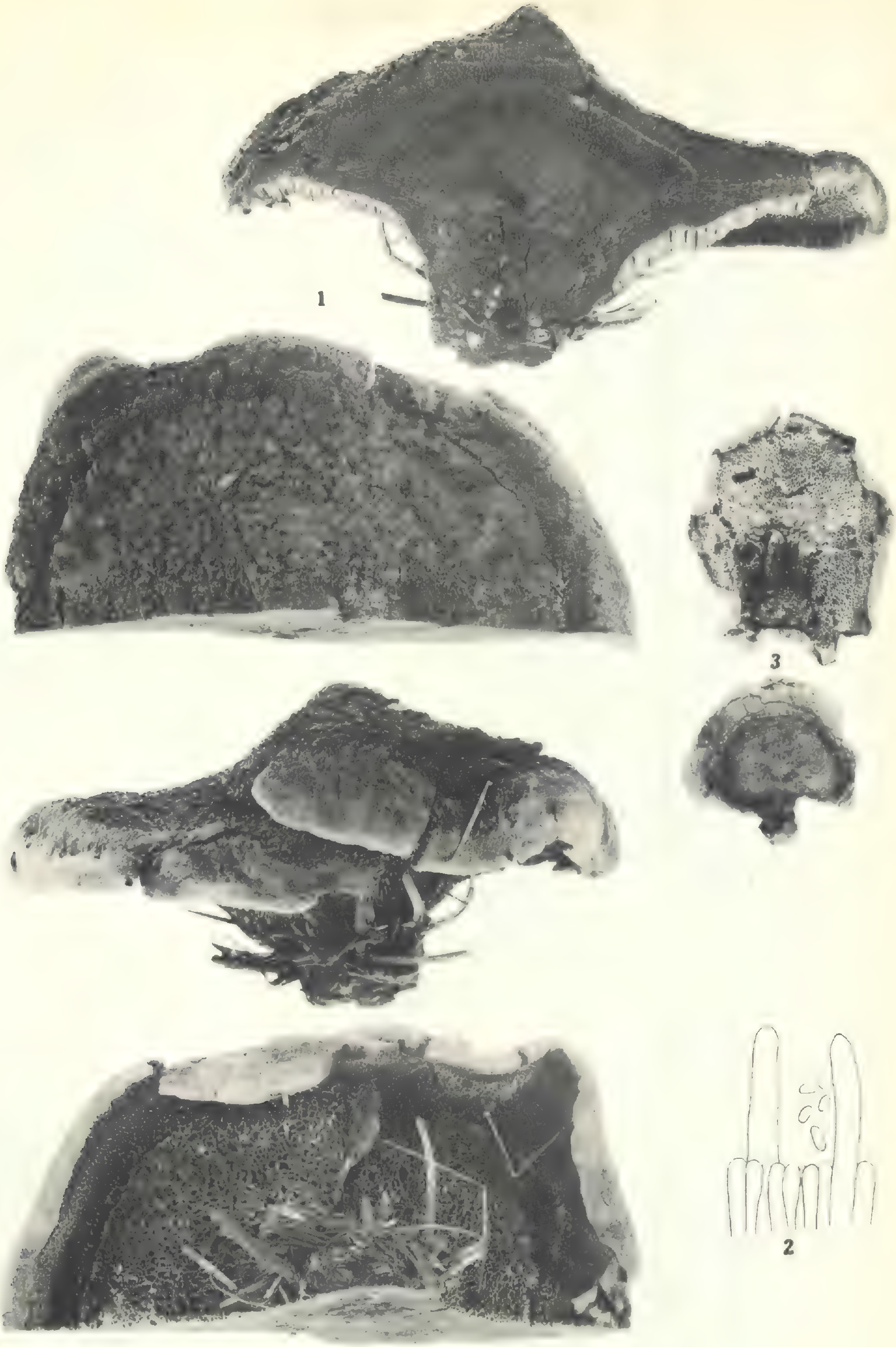
COCKAYNE, BOSTON

Explanation of Plate

PLATE 25

Figs. 1–2. *Polyporus Schweinitzii* Fr. Fig. 1 shows four different views. × 1. Fig. 2 shows spores and cystidia. × 450.

Fig. 3. *Polyporus cryptopus* Ell. & Barth. Upper and lower surfaces. × 1.



SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 26

Figs. 1–2. *Polyporus circinatus* Fr. Fig. 1 shows four sporophores, two of which are shown in vertical section. × 1. Fig. 2 shows a seta and spores. × 450.

Fig. 3. *Polyporus perennis* (L.) Fr. × 1. Five sporophores are shown of which one is in vertical section.

SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

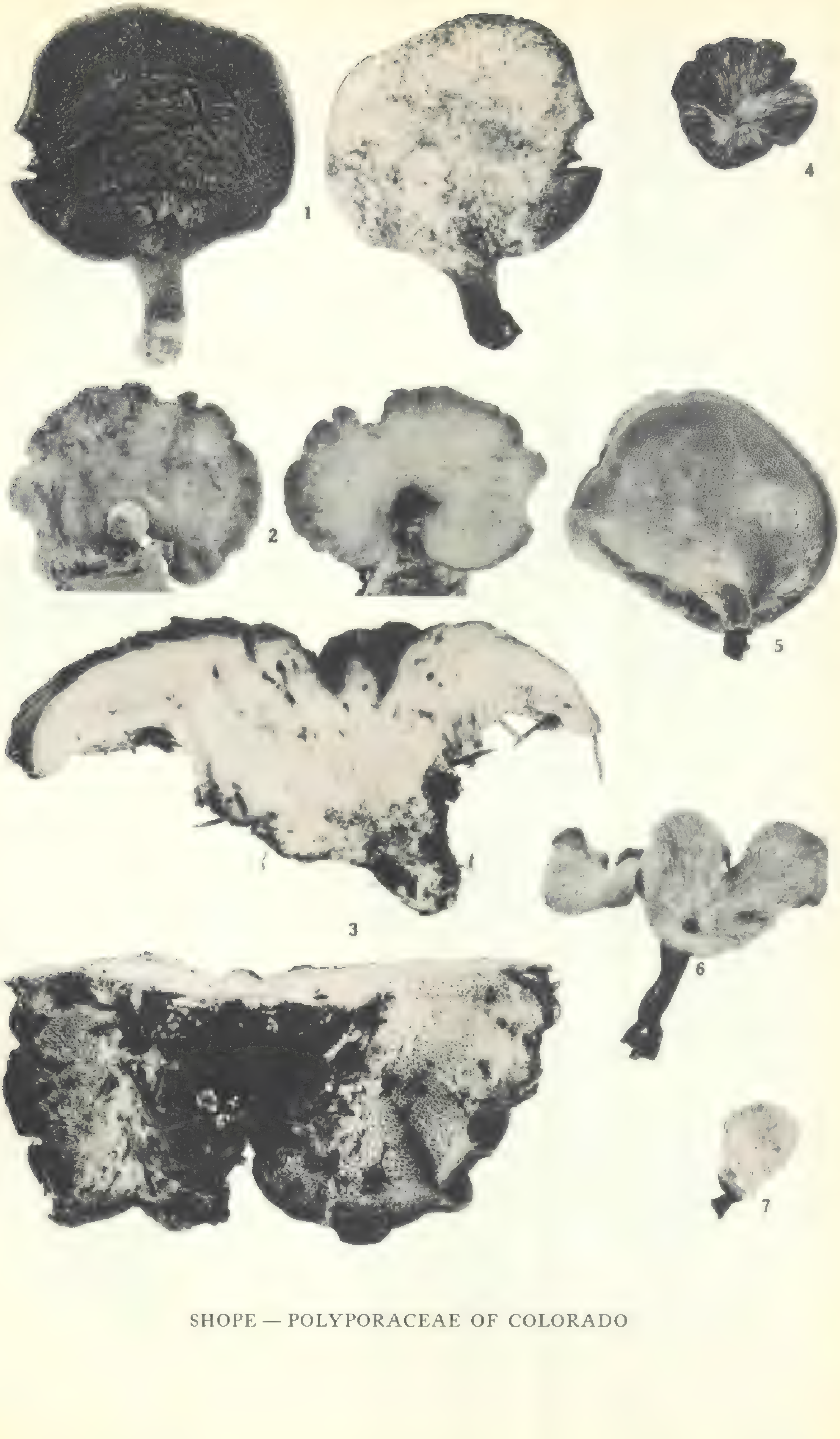
Explanation of Plate

PLATE 27

Figs. 1–2. *Polyporus elegans* (Bull.) Fr. × 1. Fig. 1 shows the upper and lower surfaces of old and weathered sporophores; fig. 2 shows young sporophores.

Fig. 3. *Polyporus hirtus* Quél. × 1. Vertical-section and pore-surface views are shown.

Figs. 4–7. *Polyporus varius* (Pers.) Fr. Young sporophores are shown in various views.



SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 28

Fig. 1. *Polyporus confluens* (Alb. & Schw.) Fr. × 1. Pore-surface and vertical-section views are shown.

Fig. 2. *Polyporus spumeus* (Sow.) Fr. × 1. Vertical-section and pore-surface views are shown.

Fig. 3. *Polyporus caesius* (Schrad.) Fr. × 1. Upper- and lower-surface views are shown.

Figs. 2–3 are from photographs by L. O. Overholts.

SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

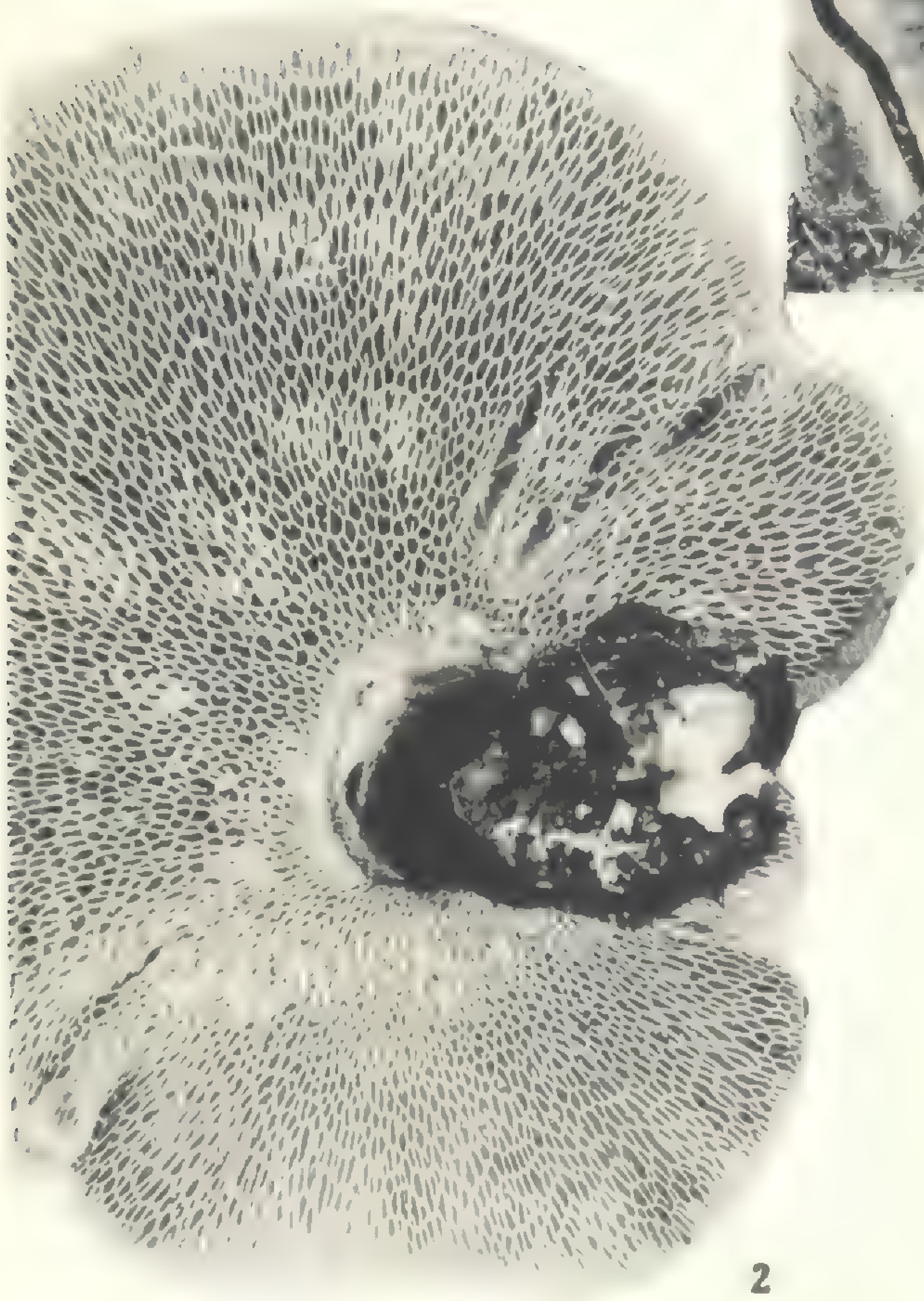
PLATE 29

Figs. 1–2. *Polyporus squamosus* (Huds.) Fr. Fig. 1 shows a habit view. × ½. Fig. 2 shows the pore surface and stipe. × 1.

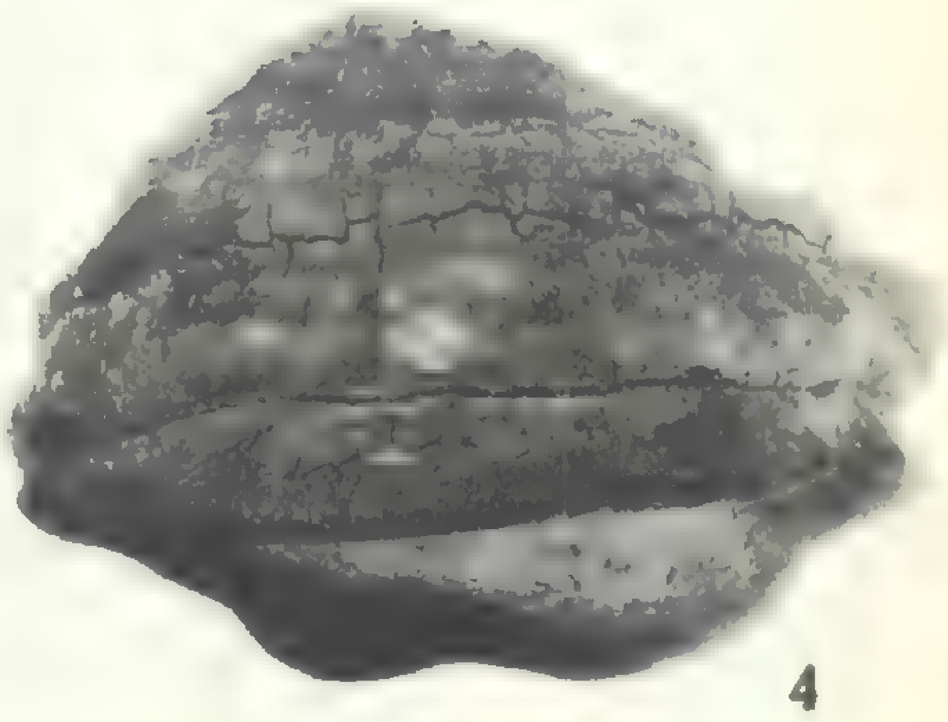
Fig. 3. *Polyporus osseus* Kalchbr. × 1. Photograph by C. G. Lloyd, courtesy of the Smithsonian Institution.

Figs. 4–6. *Fomes roseus* (Alb. & Schw.) Cooke. × 1. Surface, pore-layer, and vertical-section views are shown.

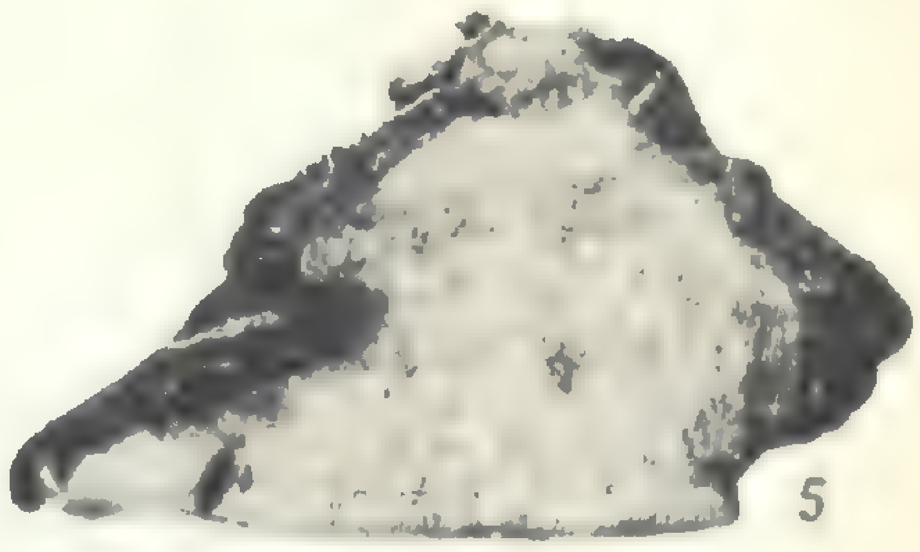
1



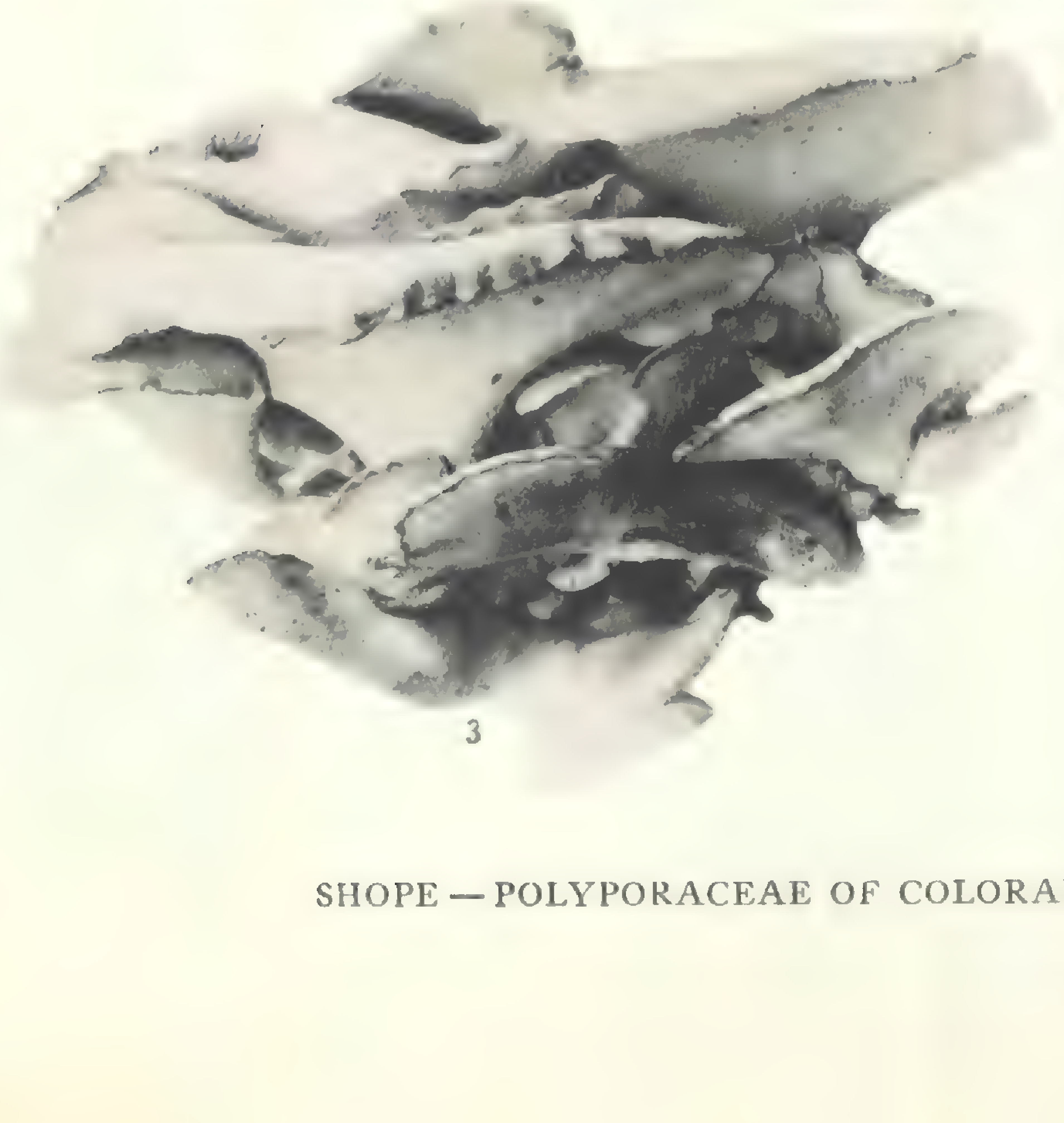
2



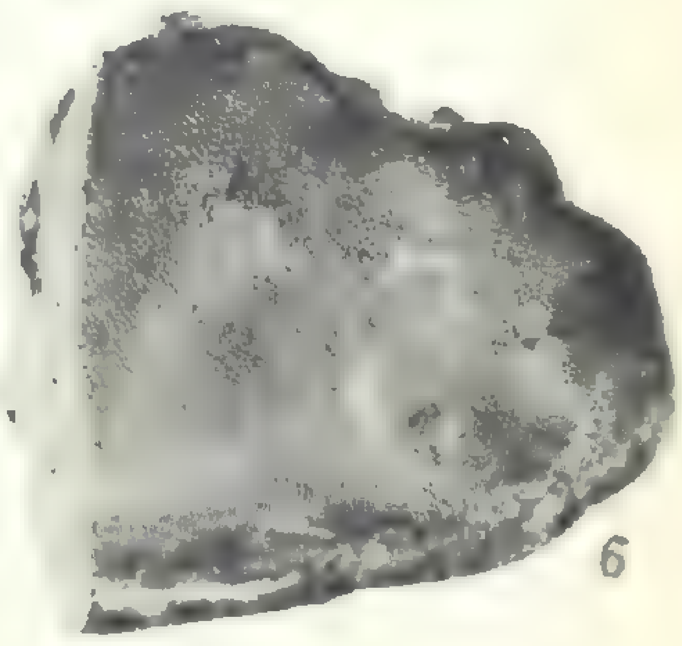
4



5



3



6

SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

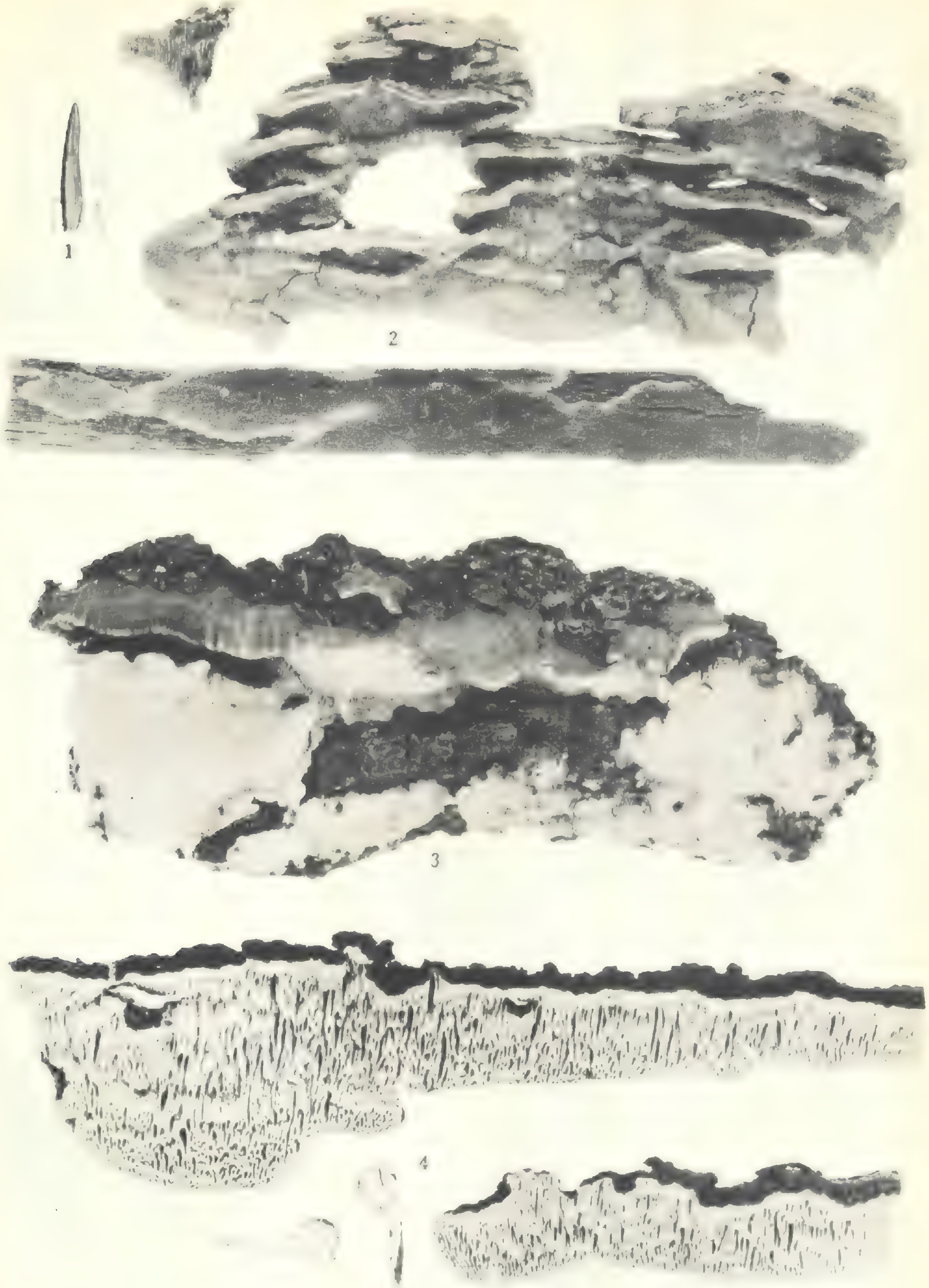
Explanation of Plate

PLATE 30

Figs. 1–2. *Trametes isabellina* Fr. Fig. 1 shows a seta and spores. × 450. Fig. 2 shows imbricate and sessile growth-forms. × 1.

Fig. 3. Habit view of *Trametes serialis* Fr. × 1.

Fig. 4. *Trametes variiformis* Pk. × 1.



SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

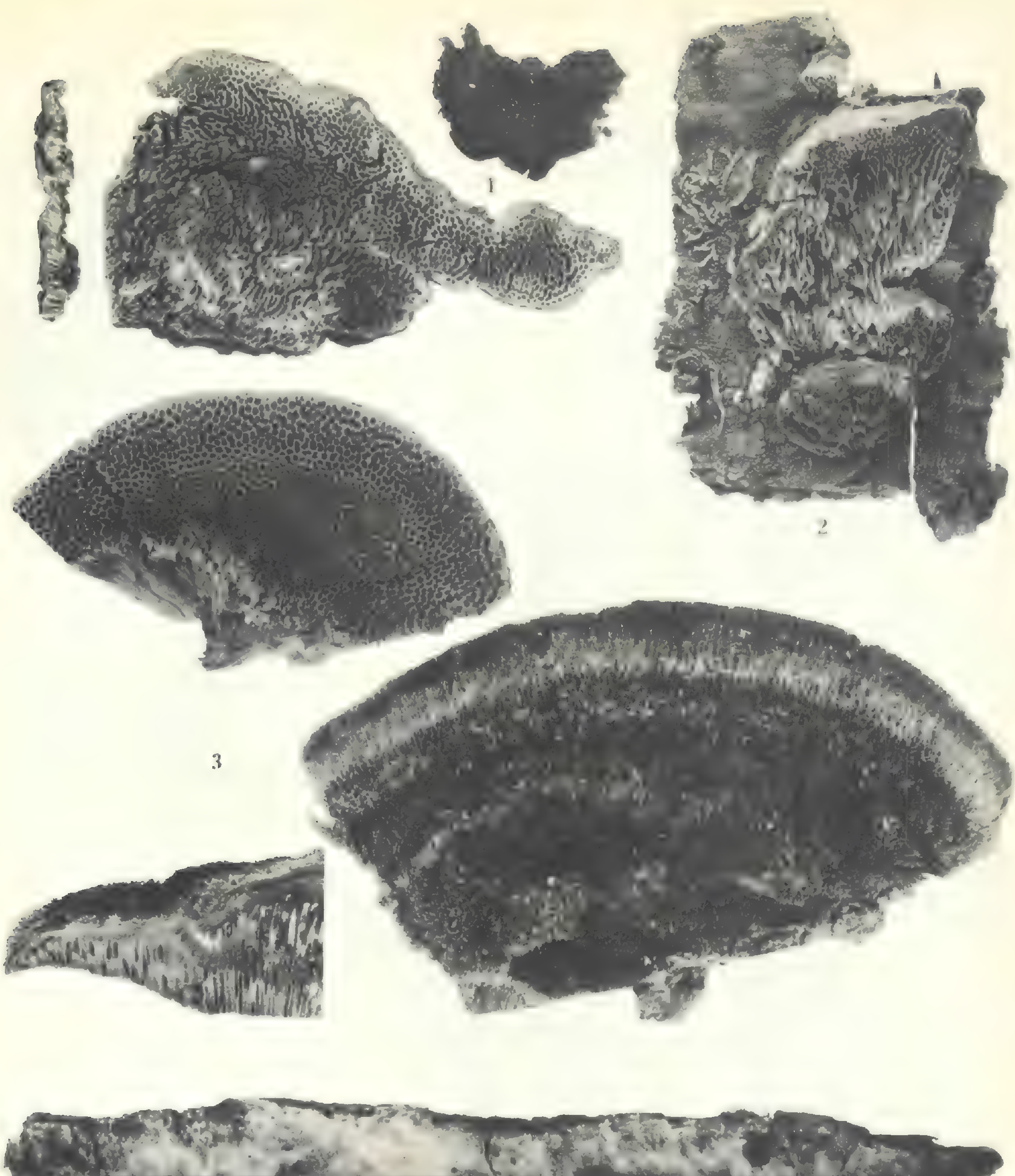
PLATE 31

Fig. 1. *Trametes stereoides* (Fr.) Bres. × 1. Upper and lower surfaces and vertical section are shown.

Fig. 2. Habit view of *Trametes heteromorpha* (Fr.) Lloyd. × 1.

Fig. 3. *Trametes hispida* Pass. × 1. Upper and lower surfaces and vertical section are shown.

Fig. 4. *Trametes odorata* (Wulf.) Fr. × 1. Upper and lower surfaces and vertical section are shown.



SHOPE—POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 32

Fig. 1. Upper and lower surfaces of *Trametes subrosea* Weir. × 1.

Figs. 2–3. *Fomes Pini* (Thore) Lloyd. Fig. 2 shows front view. × ½. Fig. 3 shows a seta and spores. × 450.

Fig. 4. *Ganoderma applanatum* (Pers.) Pat. × 1. Upper and lower surfaces and vertical section are shown.

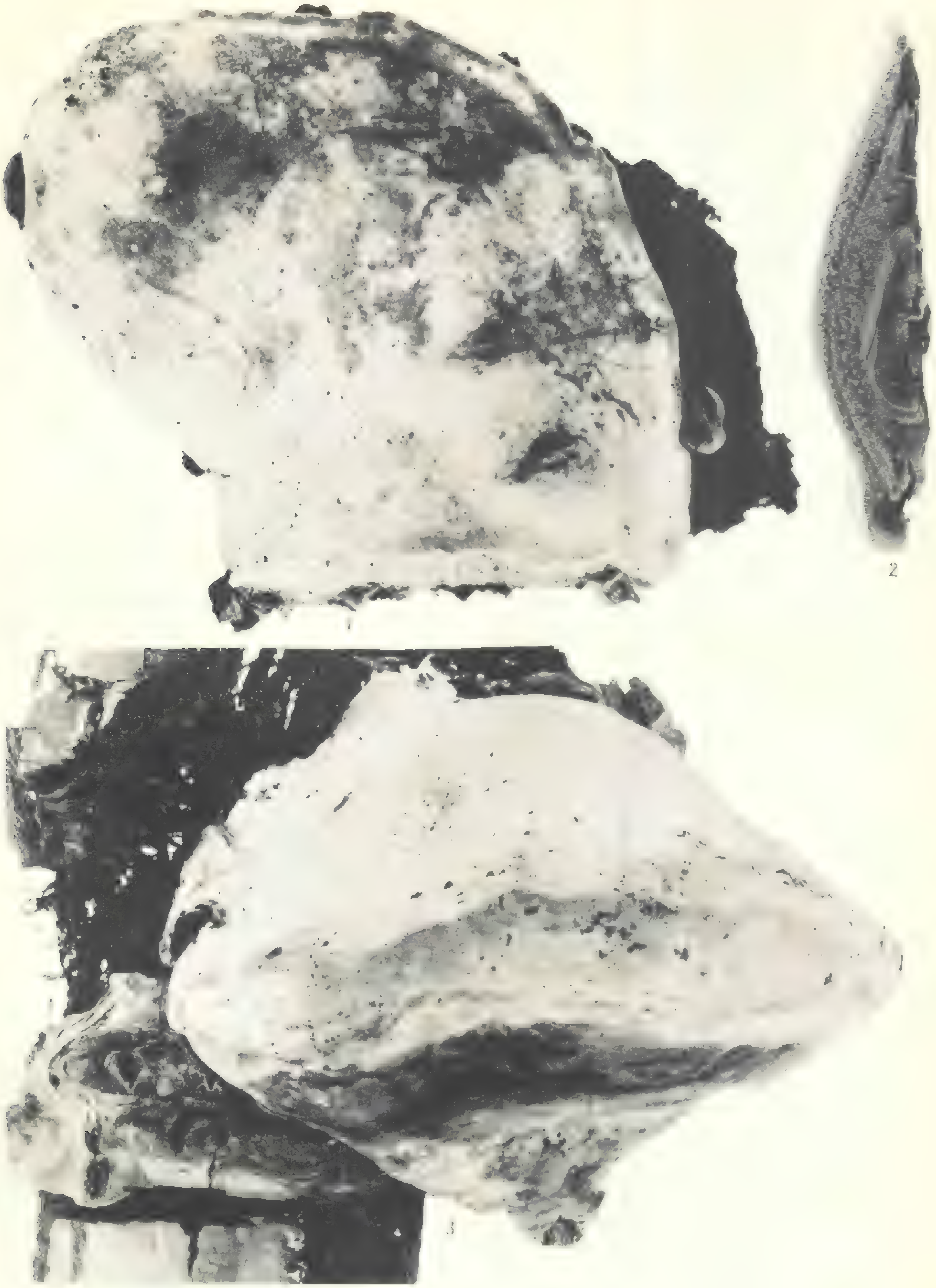
SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 33

Figs. 1–3. *Fomes pinicola* (Sw.) Cooke. × 1. Fig. 1 shows pore surface of resupinate plant; fig. 2 shows vertical section; and fig. 3, habit view of a sporophore on aspen.



SHOPE—POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

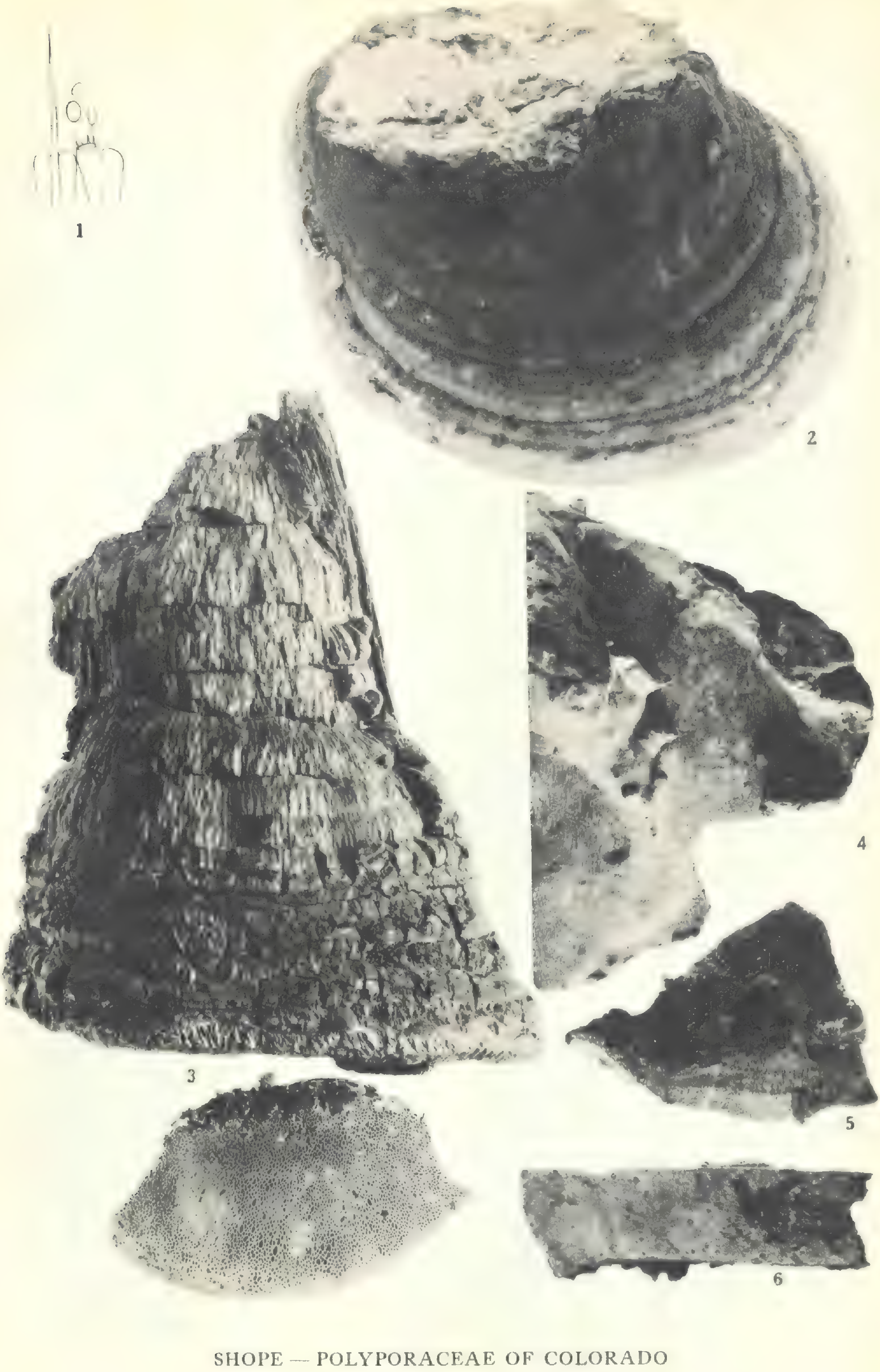
EXPLANATION OF PLATE

PLATE 34

Figs. 1–2. *Fomes pinicola* (Sw.) Cooke. Fig. 1 shows a cystidium, spores, and a basidium. × 450. Fig. 2, the resinous coating on the upper surface of a sporophore from a coniferous host.

Fig. 3. *Fomes Demidoffii* (Lév.) Sacc. & Syd. × 1. The surface and pore layer are shown.

Figs. 4–6. *Fomes fulvus* (Scop.) Gill. × 1.



SHOPE — POLYPORACEAE OF COLORADO

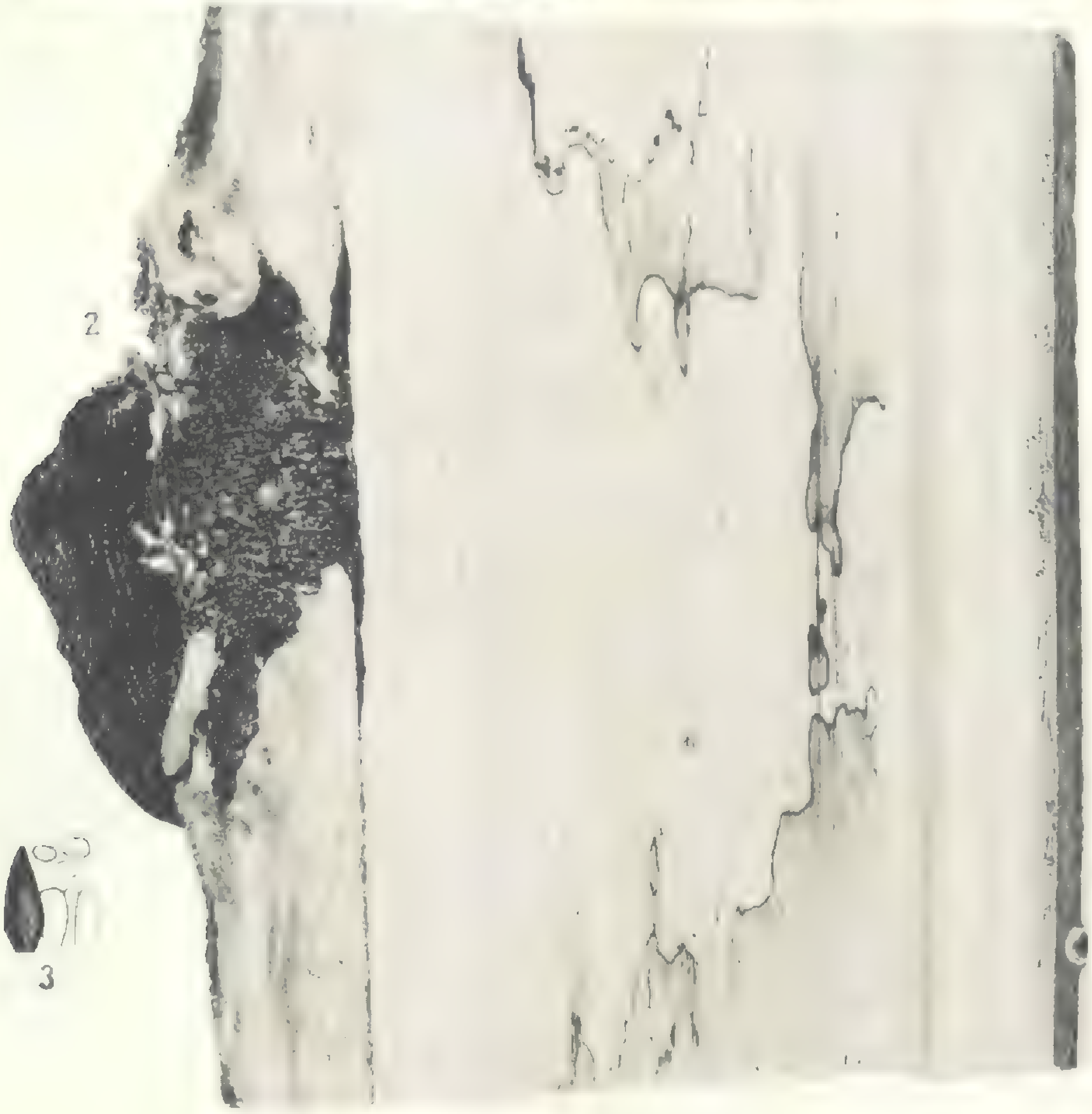
COCKAYNE, BOSTON

Explanation of Plate

PLATE 35

Figs. 1–3. *Fomes igniarius* (L.) Gill. Fig. 1 shows this fungus growing on aspen. Fig. 2 shows a longitudinal section of rotted aspen wood with a sporophore attached. × 1. Fig. 3 shows a seta and spores. × 450.

1



2

3

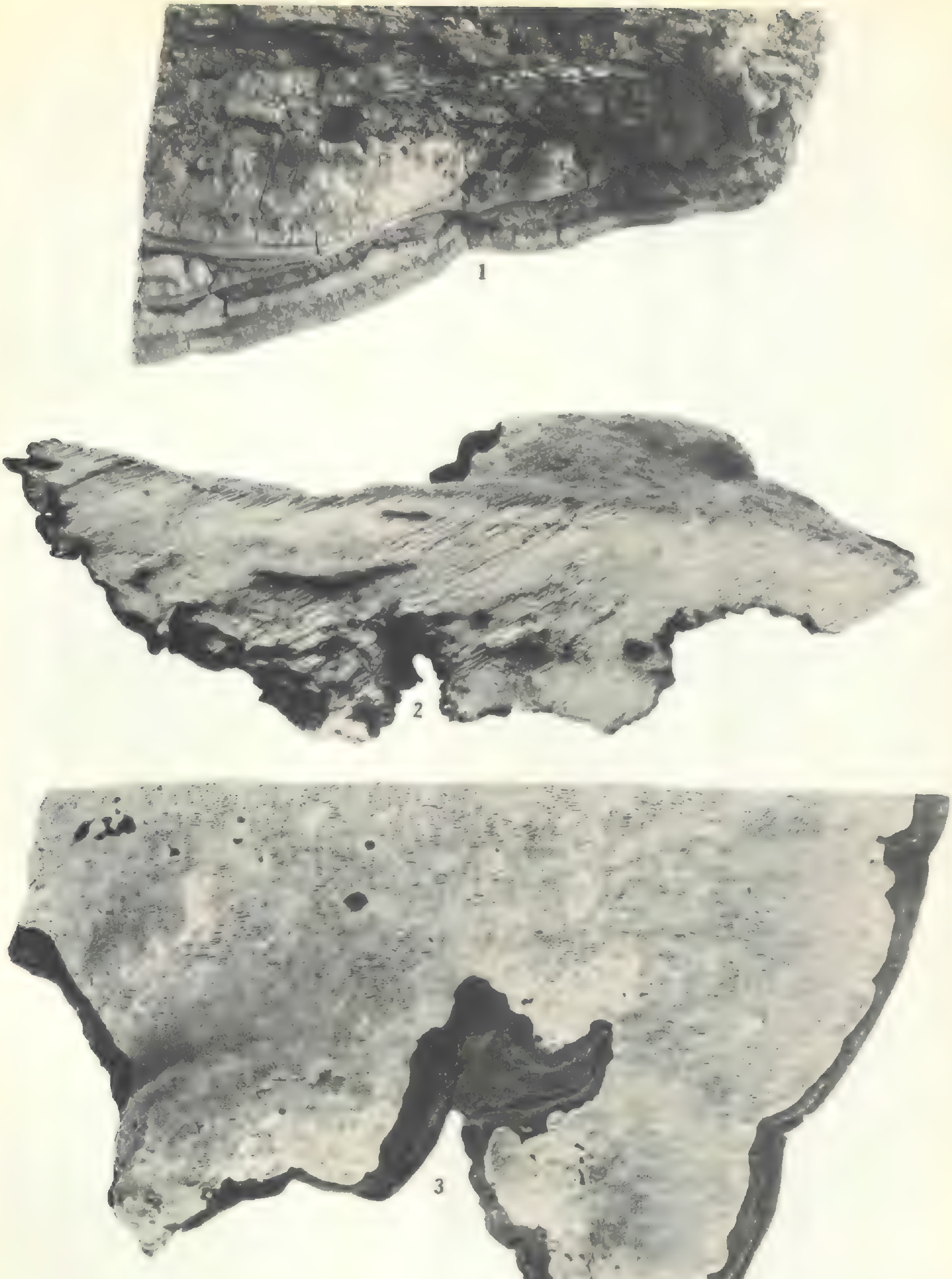
SHOPE—POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 36

Figs. 1–3. Various views of *Fomes annosus* (Fr.) Cooke. × 1.



SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

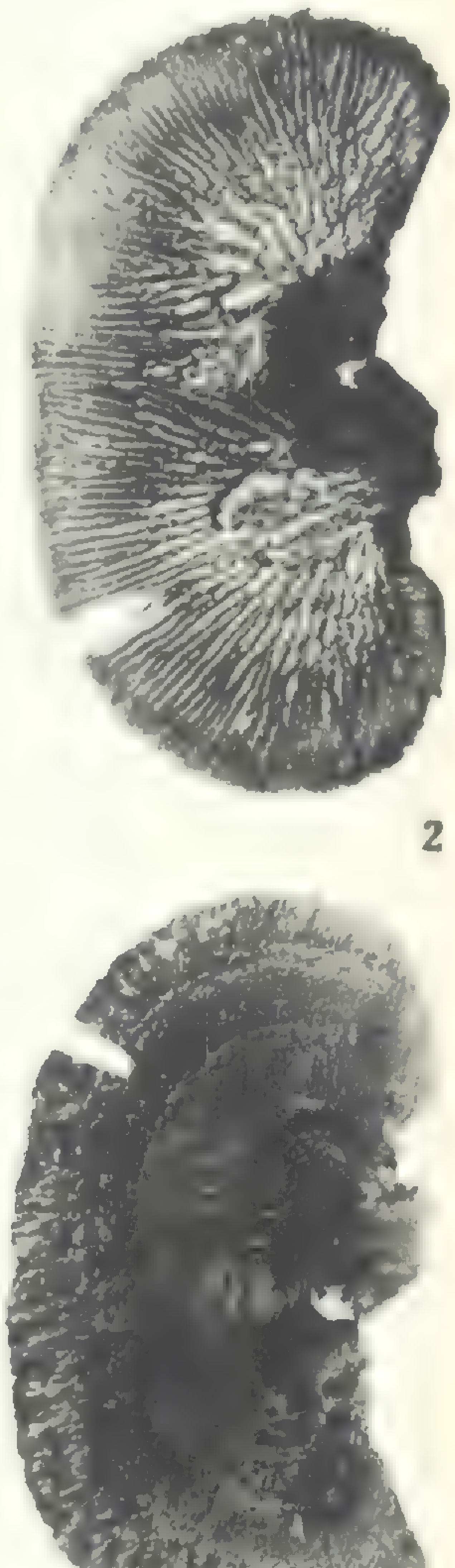
PLATE 37

Fig. 1. *Lenzites saepiaria* (Wulf.) Fr. × 1. Three sporophores showing upper and lower surfaces, and places of attachment to the substrata.

Fig. 2. *Lenzites abietinella* (Murr.) Sacc. & Trott. = *L. saepiaria* (Wulf.) Fr. × 1. Upper and lower surfaces of type.

Fig. 3. *Fomes fraxinophilus* forma *Ellisianus* (And.) Baxter. × 1. Habit and pore layer.

1



2

3

SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

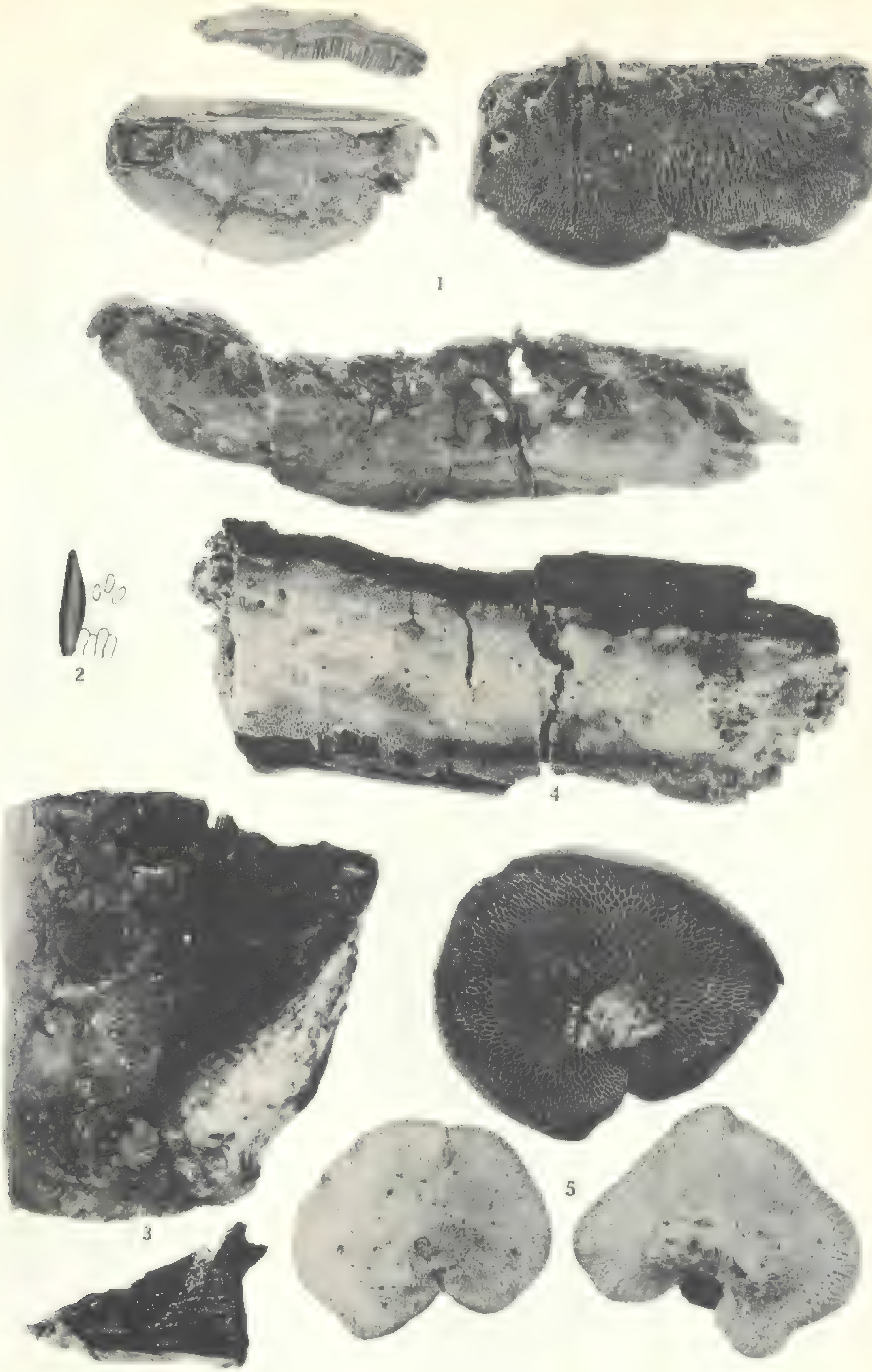
PLATE 38

Fig. 1. *Lenzites trabea* (Pers.) Fr. × 1. Two upper surface views, one lamellae surface view, and one section view.

Figs. 2–3. *Fomes nigrolimitatus* (Rom.) Egel. × 1. Fig. 2 shows a seta and spores. × 450. Fig. 3 (upper) is a habit view showing the upper surface and the pore layer, also (lower) a vertical section.

Fig. 4. *Poria monticola* Murr. × 1.

Fig. 5. *Favolus alveolaris* (DC.) Quél. × 1. Three sporophores showing upper and lower surfaces.



SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 39

Fig. 1. *Poria spissa* (Schw.) Cooke. × 1. Pore view and section view.
Fig. 2. *Poria vaporaria* (Fr.) Cooke. × 1.
Fig. 3. *Poria subacida* (Pk.) Sacc. × 1.
Fig. 4. *Poria medulla-panis* (Jacq.) Pers. × 1.
Fig. 5. *Poria ferruginosa* (Schrad.) Pers. × 1.

SHOPE — POLYPORACEAE OF COLORADO

COCKAYNE, BOSTON

ALPOVA, A NEW GENUS OF RHIZOPOGONACEAE, WITH FURTHER NOTES ON LEUCOGASTER AND ARCANGELIELLA

CARROLL W. DODGE

Mycologist to the Missouri Botanical Garden
Professor in the Henry Shaw School of Botany of Washington University

In the summer of 1930, Dr. Alfred H. Povah, of the Isle Royale Lake Superior Survey, made several collections of a very puzzling member of the Hymenogasteraceae (*sensu latiore*). This fungus, which has been referred to a new genus, is very curious in uniting the peridial characters of *Hysterangium* with the gleba of *Leucogaster*, the scattered basidia of *Melanogaster*, and the spores of *Rhizopogon*. This genus should be placed in the Rhizopogonaceae of the author.[1]

Before discussing the morphology of *Alpova* in detail it might be of interest to turn our attention to the main evolutionary tendencies which have been at work in the Gasteromycetes, a seemingly highly specialized group which has developed quite independently of the Hymenomycetes, although it must be admitted that some members bear a striking resemblance to the Agaricaceae. The writer prefers to regard this as a convergence phenomenon connected with spore dispersal rather than of phylogenetic significance. If one considers the gasteromycetous condition of certain Boletaceae, one is tempted to consider the Gasteromycetes the more primitive group and that perhaps the Agaricales have developed from them.

As a working hypothesis, it seems probable that the following statements are true:

1. The primitive Gasteromycetes consisted of spherical or somewhat irregular fructifications with no differentiated sterile tissues and no stipe, the rhizomorphs on which the fruit-bodies were borne ending at the peridium. Gradually a cushion was formed at the point of attachment from which the larger tramal plates originated. This increased in size, penetrating farther into

Issued October 28, 1931.

[1] Dodge, C. W. Gasteromycetes in Gäumann & Dodge, Comparative morphology of fungi, pp. 468–470. New York, 1928.

the fructification until it fused with the peridium at its tip, forming a percurrent columella. Along with this development, the end of the rhizomorph developed a stipe to raise the fertile portion of the fructification above the substrate for better dispersal of spores.

2. The primitive peridium consisted of a single layer of hyphal tissue rather loosely woven. The additional layers have been developed in connection with more highly specialized fructifications in response to a more rigorous environment or to secure more efficient dispersal of spores.

3. The primitive gleba consisted of a loose, indefinite tramal tissue in which conidia, as well as the basidia, were borne. As the conidia lost their main function and degenerated *in situ,* they formed a gel which nourished the developing basidium and spores. In time they disappeared and left cavities in the gleba at approximately the same time that the basidia became organized in hymenia.

4. The primitive basidium was an eight-spored stichobasidium which gradually shortened its axis and became a chiastobasidium, reducing its spore number in many groups to four and in a few species to one.

5. The primitive spore was smooth, generally ellipsoidal and hyaline, and symmetrically placed at the tip of the sterigma. Spore discharge was at first effected by the degeneration of the basidium or the rupture of the sterigma, perhaps by increasing pressure in the basidium. In many of the more primitive Gasteromycetes, portions of the broken sterigmata may still be seen attached to the spore. The hymenomycetous type has progressed still farther with a highly developed mechanism for the discharge of an asymmetrically placed spore, so accurately described by Buller.[2] This hymenomycetous type is so fixed that it persists even in the gasteromycetous condition of *Boletinus decipiens* (Berk. & Curtis) Peck, where nearly all the other hymenomycetous characters have completely disappeared.

While the foregoing statements seem to be true, one sometimes finds an obviously highly developed form which has retained some primitive character, e. g., the basidium and spores of the Phal-

[2] Buller, A. H. R. Researches in fungi 3: 1–496. 1924.

laceae remain comparatively primitive whereas the tissues of the fructification have been highly specialized, even to the extent of securing insect dispersal of the spores.

When we turn our attention to *Alpova* in the light of the foregoing discussion, we find a very primitive member of the Rhizopogonaceae. The peridium is pseudoparenchymatous, of large, thin-walled cells, a character which our working hypothesis considers rather advanced, especially since it is comparatively rare elsewhere in the family. The trama, too, is composed of large, thin-walled, parallel hyphae, giving it a pseudoparenchymatous appearance. However, we have no highly differentiated sterile tissues.

The basidia are irregularly distributed through the fertile tissue between the layers of trama, apparently rising from large thin-walled hyphae from the trama which penetrate the gel formed by the decaying conidia (?). In *Leucogaster* we have a similar gel, but the basidia, although long-pedicellate, are always developed directly from the trama and form a loose hymenium. On the other hand, in the highly developed Podaxaceae, in both *Phellorinia* and *Podaxis* we have the basidia borne in compact clusters from small funiculi of large thin-walled hyphae (see pl. 40, fig. 6, for appearance of *Podaxis Farlowii*[3]).

The curious structures which form the gel into which the basidia grow are still unexplained. E. Fischer[4] considered them large sterile cells formed in the ground tissue as a kind of pseudoparenchyma in an early stage of *Leucogaster floccosus* Hesse, whereas the writer,[5] in view of the curious way in which they are borne, considered them to be vestigial conidia which may have lost their original function. Plate 40, fig. 4, shows a somewhat similar organ in an otherwise degenerated "cavity" of *Alpova*. Whether the much larger hyaline spheres also found in the fertile tissues of *Alpova* are borne in this manner is uncertain, since I have not been able to find their points of attachment.

[3] I am deeply indebted to Miss Elizabeth Morse of the University of California for excellent material of both *P. Farlowii* Massee, from which these figures were made, and of *P. anomalus* Lloyd, which shows the same condition.

[4] Fischer, E. Mykologische Beiträge, 25. Jugendstadien des Fruchtkörpers von Leucogaster. Naturf. Ges. Bern, Mitt. **1921**: 301–307 [20–26]. 1922.

[5] Zeller, S. M. & C. W. Dodge. Leucogaster and Leucophlebs in North America. Ann. Mo. Bot. Gard. **11**: 390–391. 1924.

The basidium of *Alpova* is especially interesting in that it is always eight-spored, which would point to a very primitive condition if we accept the hypothesis that the basidium and the ascus have been derived from a common ancestor after the number of ascospores in the ascus had been fixed at eight.[6] Eight spores per basidium is a very rare phenomenon in the Basidiomycetes, and I know of very few species where the number seems so fixed as in *Alpova*. In the Gasteromycetes, however, there are many species with basidia bearing more than four spores, as well as several species where occasionally or regularly only one very large spore is borne. In species where the number of spores has been fixed at four, many cases have been reported where the spore nucleus divides promptly, producing a binucleate spore. Hence it appears that meiosis immediately followed by a vegetative division giving eight nuclei is still fixed in the Gasteromycetes, although it is very rare in the Hymenomycetes.

The basidium of *Alpova* is long and slender, apparently of the stichobasidial type, although I have not had the opportunity to observe nuclear divisions in it. This type is apparently very rare in the Gasteromycetes, occurring only in a few American species of *Leucogaster*, whereas the other species of that genus appear to be of the chiastobasidial type. The occurrence of basidia on long, slender funiculi which traverse the fertile region is suggestive of conditions found in the Podaxaceae. In the latter, however, the basidium has already become four-spored with a thick-walled, colored spore, has shortened its long axis as a chiastobasidium (see pl. 40, fig. 7, *Podaxis Farlowii*), and assembled in dense tufts about nodes of the funiculi, whereas in *Alpova* the basidia are borne singly along the funiculi.

The spores of *Alpova* are ellipsoidal with a slightly thickened, smooth wall, hyaline under the microscope but colored brownish in mass, very much like *Rhizopogon* but much smaller in our species. This tiny ellipsoidal to bacilliform spore has been retained by several genera of lower Gasteromycetes and by the highly specialized Nidulariaceae, Phallaceae, and Clathraceae.

[6] Gäumann, E. A. Vergleichende Morphologie der Pilze. pp. 399–401. Jena, 1926.

ALPOVA gen. nov.

Fructificationes sphaericae, sine columella, sine stipite; gleba gelatinosa, locelli impleti, basidia in funiculis per locellos vagantibus, octospora; sporae ellipsoideae.

Alpova cinnamomeus Dodge, sp. nov. Pl. 40, figs. 1–5.

Fructificationes sphaericae, 5–20 mm. diametro metientes, cinnamomeae; peridium 300 μ crassitudine, cellulis magnis pseudo parenchymate; gleba cinnamomea, gelatinosa; locelli cellulis magnis qui in gelatina dilabunt, impleti; septa tenuia, 25–50 μ crassitudine pseudoparenchymate vel hyphis magnis parallelis qui pseudoparenchymatem simulant; basidia in funiculis hypharum magnarum per locellos vagantibus, longissima, 20 x 22 x 4–5 μ, octospora, sterigmatibus curtis; sporae hyalinae sub lente, cinnamomeae acervatae, ellipsoideae, 3–4 x 1.5–2.5 μ.

Type: Tobin Harbor trail, Isle Royale, Michigan, *C. A. Brown Fp. 73*, in Herb. Univ. Michigan.

Fructifications spherical, 5–20 mm. in diameter, pinkish buff to cinnamon buff, turning hazel to auburn (Ridgway); peridium thick, 300 μ, composed of large-celled pseudoparenchyma; gleba clay-color, turning Hessian brown, gelatinous, the spaces between the septa at first filled with large spherical cells (conidia?) which finally disintegrate; septa of large, thin-walled, hyaline, parallel hyphae which simulate pseudoparenchyma; basidia on slender funiculi as in the Podaxaceae, scattered irregularly in the gel, very long and slender, 20–22 x 4–5 μ, eight-spored with sterigmata about 1 μ long; spores hyaline under the microscope, pale brown in mass, ellipsoidal, 3–4 x 1.5–2.5 μ.

Half buried in soil, often under *Alnus*, Isle Royale, Lake Superior, July to September.

In view of the frequent affinities which plants of this region show with those of the Pacific slope, it is interesting to note that the species of *Leucogaster* to which this species appears most closely related are all Californian.

Specimens examined:

Michigan: Isle Royale, Tobin Harbor, *C. A. Brown Fp. 28, 73* type; Rock Harbor Trail, *A. H. Povah & G. L. Lowe Fp. 92, C. A. Brown Fp. 298;* Siskowet Outlet at Siskowet Bay, *A. H. Povah Fp. 635* (in Herb. Univ. Michigan).

During a recent visit to the herbaria of Europe the writer was able to study the types of most of the species of the Hymenogasteraceae. The following notes on synonymy of *Leucogaster* may

be of interest in this connection, since the genus seems so closely allied to *Alpova.*

Leucogaster nudus (Hazslinszky) Hollós, Mus. Nat. Hungarici Ann. **6:** 319. 1908; Magyarorszag Földalatti Gombai, 98, 208. 1911 (excl. syn.).

Hydnangium nudum Hazslinszky, K. K. Zool.-bot. Ges. Wien, Verhandl. **25:** 64–65. 1875; Magyar Tudomanyos Akad. Termeszettud. Közl. **13:** (9). 1875 [often cited as Magyarhon hasgombai, 9. 1876]; Hedwigia **16:** 44. 1877; Saccardo, Syll. Fung. **11:** 172. 1895.

Hydnangium virescens Quélet, Soc. d'Émul. Montbéliard Mem. 1875 [Champ. Jura et des Vosges **3:** 110. 1875]; Enchiridion, 248. 1886; DeToni in Sacc. Syll. Fung. **7:** 177. 1888.

Leucogaster luteomaculatus Zeller & Dodge, Ann. Mo. Bot. Gard. **11:** 394–395. 1924.

Type: cotype in Berlin. Authentic material of *Hydnangium virescens* collected at Waiter in the Vosges by Solms-Laubach and determined by Quélet in Upsala Bot. Mus. Inquiry in France failed to locate Quélet's herbarium if he left one. However, there is much material and many paintings in the Elias Fries Herbarium in Upsala. Apparently the situation is much the same here as in the case of Elias Fries' Swedish species, which are much more fully represented in the M. J. Berkeley Herbarium at Kew than they are in his own herbarium at Upsala. Type of *Leucogaster luteomaculatus* in the Farlow Herbarium at Harvard University.

L. citrinus (Harkness) Zeller & Dodge.

This species has also been seen from Mt. Lofty, South Australia, *J. B. Cleland 4*, not previously known outside California.

A study of all the types involved shows that the following species of *Octaviania* and *Hydnangium* should be transferred to *Arcangeliella.* The group of species centering about *Arcangeliella Stephensii* is separable with difficulty, and it is quite possible that they should be considered only varieties.

Arcangeliella rosea (Harkness) Zeller & Dodge, n. comb.

Octaviania rosea Harkness, Cal. Acad. Sci. Bull. **1:** 29. 1884.

Type: in Dudley Herb. at Leland Stanford Jr. University.

A. Stephensii (Berk. & Br.) Zeller & Dodge, n. comb.

Hydnangium Stephensii Berk. & Br. Ann. & Mag. Nat. Hist. I. **13**: 352. 1844.—*Octaviania Stephensii* Tulasne, Fung. Hypog. 78. 1851.—*Octavianina Stephensii* O. Kuntze, Rev. Gen. Pl. 3^2: 501. 1898.

Type: in Kew, British Museum, and in Museum d'Histoire Naturelle de Paris.

A. Ravenelii (Berk. & Curtis) Dodge, n. comb.

Octaviania Stephensii v. *Ravenelii* Berk & Curtis in Tulasne, Fung. Hypog. xvii. 1851.—*Hydnangium Stephensii* v. *Ravenelii* Berk. Grev. **2**: 33. 1873.—*Hydnangium Ravenelii* Berk. & Curtis in Curtis, Bot. N. Car. 110. 1867.—*Octaviania Ravenelii* Lloyd, Myc. Notes 67: 1140. 1922.

Type: in Kew, in British Museum, and at Farlow Herbarium.

A. australiensis (Berk. & Br.) Dodge, n. comb.

Hydnangium australiense Berk. & Br. Linn. Soc. London, Trans. II. Bot. **2**: 66. 1883.—*Octaviania australiensis* Cooke, Handbook Austral. Fungi, 246. 1892.—*Hydnangium brisbanense* Berk. & Br. in Cooke, Handbook Austral. Fungi, 247. 1892.—*H. glabrum* Rodway, Papers & Proc. Roy. Soc. Tasmania **1920**: 157. 1921.

Type: both *H. australiense* and *H. brisbanense* were based on the same specimen, Brisbane, *F. M. Bailey 188*, at Kew and in British Museum. Cotype of *H. glabrum* in Dodge Herb.

Explanation of Plate

PLATE 40

Figs. 1–5. *Alpova cinnamomeus* Dodge.

Fig. 1. Section of peridium, × 285.

Fig. 2. Section of fructification showing peridium and gleba. The white areas of the gleba represent the hyaline septa. × 38.

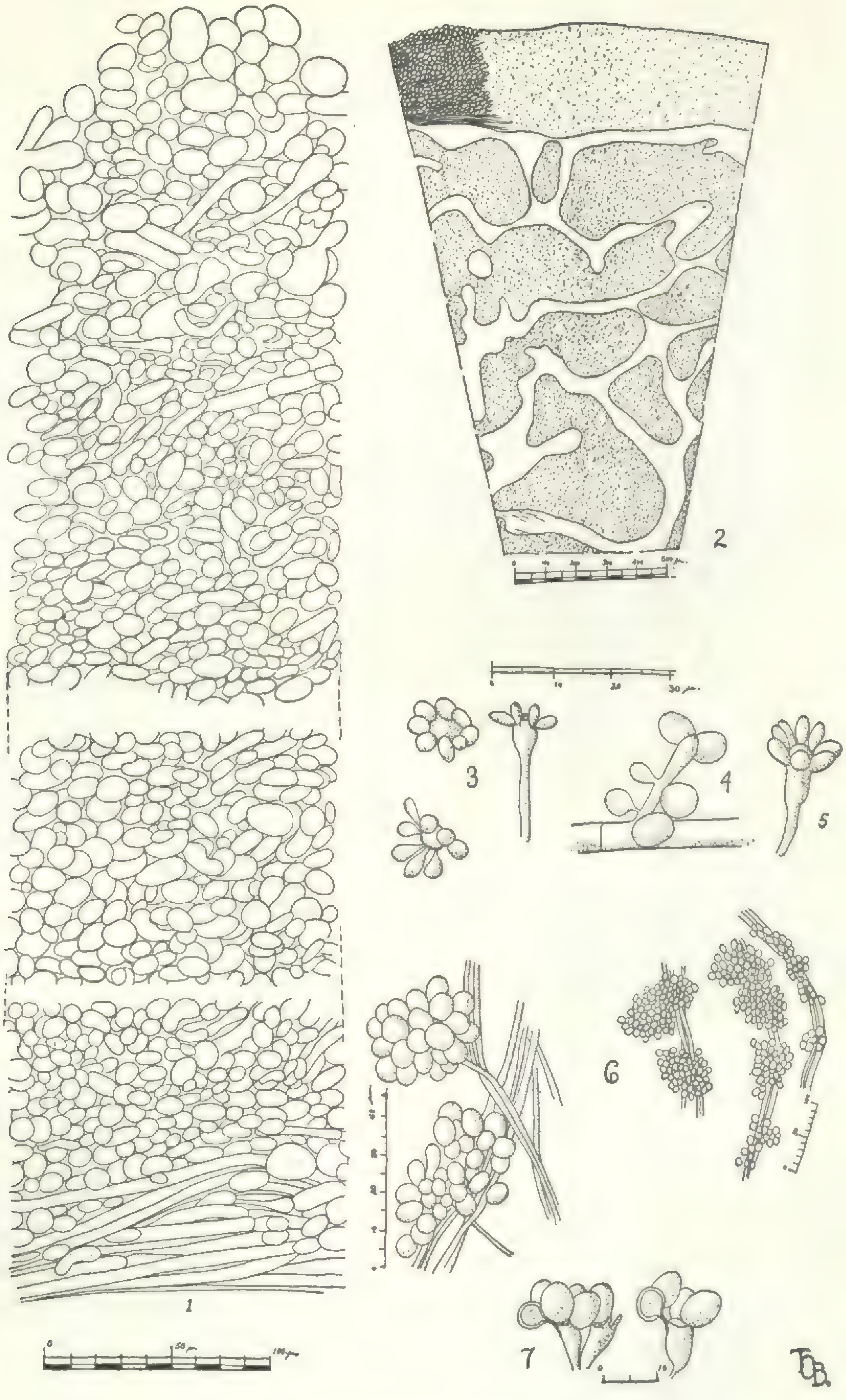
Figs. 3, 5. Basidia showing both top and side views. × 766.

Fig. 4. Hypha bearing the large thin-walled cells (conidia?) which gelify before the basidia develop. × 766.

Figs. 6, 7. *Podaxis Farlowii* Massee.

Fig. 6. Funiculi showing verticillate tufts of basidia. × 100, 433.

Fig. 7. Basidia and basidiospores. × 1400.



DODGE — ALPOVA

COCKAYNE, BOSTON

THE CHROMOSOME COMPLEMENTS OF ALLIUM STELLATUM AND NOTHOSCORDUM BIVALVE

EDGAR ANDERSON

Geneticist to the Missouri Botanical Garden
Associate Professor of Botany in the Henry Shaw School of Botany of Washington University

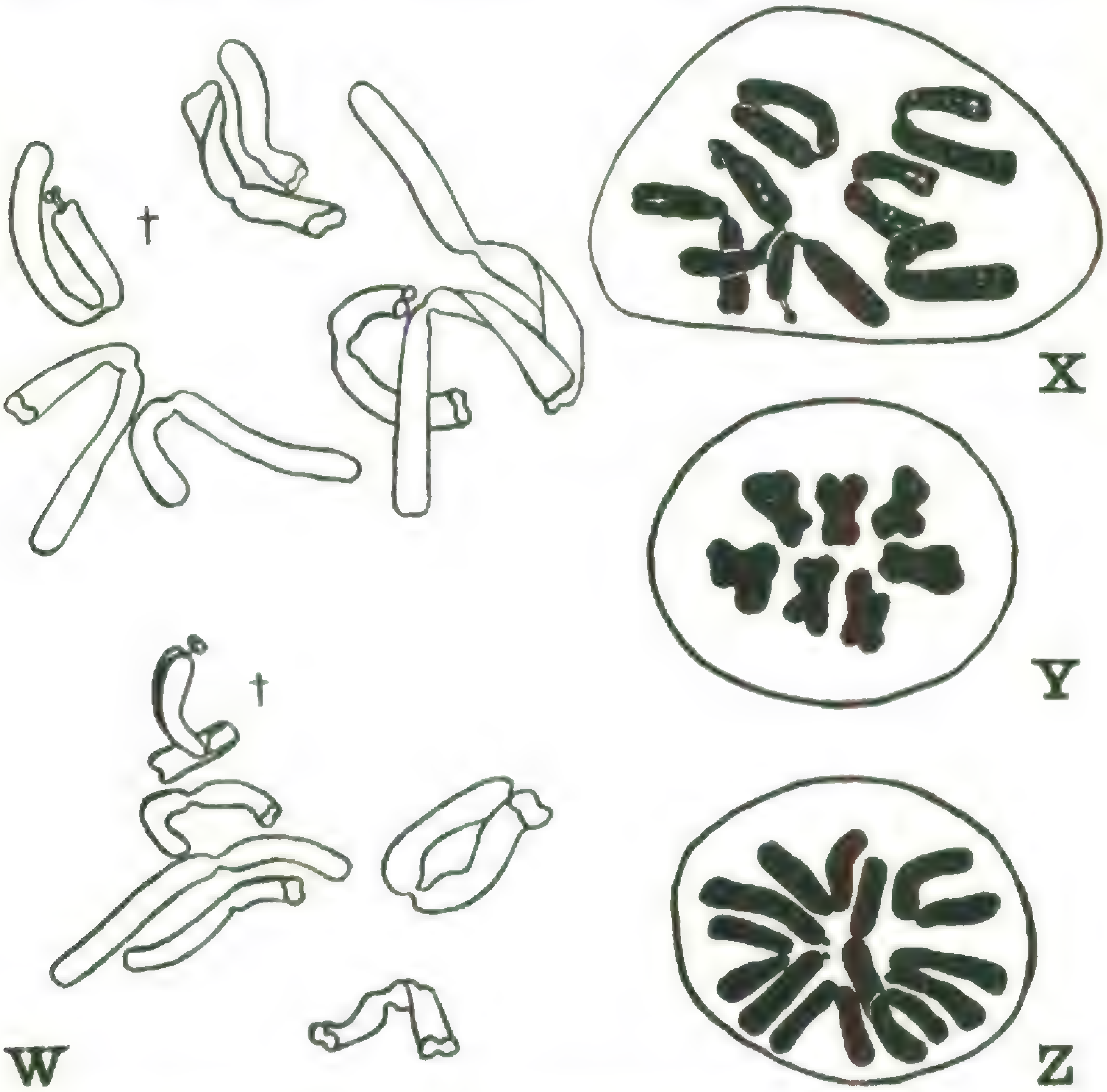
Allium stellatum Ker. is very common on dry, rocky banks from Illinois and Missouri westward. It bears large upright umbels of bright rose-pink flowers in late autumn and has six conspicuous crests on the ovary which persist in the fruit.

As might have been expected, its distinct morphological position in the genus *Allium* is reflected by its unusual chromosome number. The basic number for *Allium* is eight. Gaiser's summaries ('30, '30a) give twenty-seven species and varieties as having sixteen chromosomes (2n), and four as having 32 (2n). The only other number so far reported is seven, which was the haploid number reported for *A. ursinum* by Chodat ('25) and for *A. Moly* by Miyake ('05) and Levan ('29). The possible relationship of *Allium stellatum* to these species is uncertain, since *Allium* is a large genus badly in need of monographic treatment, and the natural relationships of the species have not been worked out.

Material was collected at Herculaneum, Missouri, and root-tips, pollen mother cells, and dividing pollen grains were examined. In the root-tips the large chromosomes nearly filled the cell at metaphase, and though there were many divisions it was difficult to find any which could be counted. Several counts were finally obtained and all gave fourteen chromosomes. The clearest is illustrated in fig. W. It will be noticed that there is one pair of chromosomes with satellites. Pollen divisions were much easier to count. All showed seven chromosomes and in many of them one chromosome was seen to bear a satellite (fig. X). All the pollen mother cells (fig. Y) showed a regular reduction division with seven pairs of conjugating chromosomes. The configurations were similar to those already published by Chodat ('25) and Levan ('29) for other species of *Allium.*

The genus *Nothoscordum* is closely related to the genus *Allium*, one of the chief differences being the lack of odor in the bulbs

and leaves of the former. Smears of young pollen grains were made from two plants of *Nothoscordum bivalve* (L.) Britton, collected at Cliff Cave, Missouri. Pollen grains of each plant were found to have nine (n) chromosomes (fig. Z), seven with median or sub-median constrictions, and two with terminal constrictions.



W, Somatic chromosomes (2n = 14) from the root-tip of *Allium stellatum*. The figure has been separated for clearness and may be reassembled by superposing the + 's.

X, Dividing pollen grain of *A. stellatum*. × 1900.

Y, Pollen mother cell of *A. stellatum*, polar view. × 1900.

Z, Dividing pollen grain of *Nothoscordum bivalve*. × 1800.

All figures drawn with camera-lucida at bench level and reduced one-half for illustration.

These latter are conspicuously marked by large, deep-staining insertion points. The chromosomes, like those of *Allium*, are large and ribbon-like. The attachment constrictions in *Allium* are usually median or sub-median (or at most sub-terminal). It

seems quite possible that *Nothoscordum* may have been derived from an eight-chromosomed parental stock by the division of one of the large median-constricted chromosomes. This is further borne out by the fact that the combined length of the two chromosomes with terminal constrictions is only a very little greater than that of the longest chromosome with a median constriction.

Bibliography

Chodat, R. ('25). La chiasmatype et la cinèse de maturation dans l'Allium ursinum. Soc. Bot. Genève, Bull. II. **17**: 1–30. 1925.

Gaiser, L. O. ('30). Chromosome numbers in Angiosperms. Bibl. Genet. **6**: pp. 388–389. 1930.

————, (30a). *Ibid.* III. Genetica **12**: p. 240. 1930.

Levan, A. ('29). Zahl und Anordnung der Chromosomen in der Meiosis von Allium. Hereditas **13**: 80–87. 1929.

Miyake, K. ('05). Über Reduktionsteilung in der Pollenmutterzellen einiger Monokotylen. Jahrb. f. wiss. Bot. **42**: 83 –120. 1905.

Explanation of Plate

PLATE 41

Fig. 1. *Allium stellatum* on limestone outcrop, Festus, Missouri.
Fig. 2. *Allium stellatum*, representative umbels.

1

2

ANDERSON—ALLIUM AND NOTHOSCORDUM

HYMENOMYCETOUS FUNGI OF SIBERIA AND EASTERN ASIA—MOSTLY OF WOOD-DESTROYING SPECIES

EDWARD ANGUS BURT

Formerly Mycologist to the Missouri Botanical Garden

The fungi enumerated in the following list were received from Professor K. E. Murashkinsky of the Siberian Agricultural Academy, Omsk, Siberia, in two lots. The first, consisting of 113 specimens, was received in February, 1928. Some of the specimens were already named, whereas others were for me to study and report results. After a report concerning this sending had been made the second and larger consignment of specimens arrived, study of which was completed recently.

The complete series of some 250 carefully selected specimens, with record for each of the botanical names of the substratum upon which growing and the widely separated localities across Siberia proper and Eastern Asia to Vladivostok, has been of great interest in extending westward the range of some species heretofore known only in the United States and in extending the eastern range of many European species. Descriptions of some of the rare and more or less imperfectly known species of Fries and of Karsten would seem in the light of these specimens to have been based on isolated gatherings from the extreme western limits of the range of each. An example of the latter is *Stereum ochroleucum* Fr., concerning which the mycologists of central and southern Europe are in error.

An early study comprising all groups of the fungi of Siberia collected by Martinoff, chiefly from the region of Minussinsk, was made by Baron de Thümen, assisted by specialists. The results were published in five parts as Thümen, 'Beiträge zur Pilz-flora Siberiens,' in Soc. Imp. Moscou Bul. Vols. 52, 53, 55 and 56, of the years 1877–1881. Saccardo published an additional list of Siberian fungi in Soc. Roy. Bot. Belg. Bul. Vol. 28, pp. 77–117. *pl. 4–6.* 1889, and included in his work a list of all the species given in the five papers by de Thümen. In the following

list, confined to Hymenomycetes and covering more equally all northern Asia rather than Minussinsk, I have checked with an asterisk * each species given before in the lists of de Thümen and Saccardo.

The collections in the Districts of Omsk, Tara, and Sajany, Siberia, were usually made by Professor Murashkinsky, those in the District Barnaoul, Siberia, by Konjev, those in District Amur, Eastern Asia, by Krawtzew, and those in District Vladivostok, Eastern Asia, by Ziling. All received are preserved in my herbarium.

AGARICACEAE

***Pleurotus applicatus** (Batsch) Berk.

On *Sorbus Aucuparia*, Altai, Asia, July 12, coll. *Murashkinsky.*

***Schizophyllum commune** Fr.

On *Picea excelsa*, District Tara, Siberia, August, coll. *Murashkinsky*, B 4.

Lenzites heteromorpha Fr.

On *Abies sibirica*, District Sajany, Siberia, August, coll. *Murashkinsky.*

Lenzites laricina Karst. Soc. pro Fauna et Fl. Fennica Acta 27^4: 4. 1905.

On *Larix sibirica*, District Sajany, Siberia, July 10, coll. *Murashkinsky*, B 9; on *Larix sibirica*, Altai, Asia, August, comm. by K. E. Murashkinsky, B 41; on *Larix dahurica*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 093.

Lenzites septentrionalis Karst.

On *Betula verrucosa*, District Tara, Siberia, June, coll. *Murashkinsky*, B 13.

Lenzites tenuis Lév.

On rotting trunks, District Vladivostok, Eastern Asia, June, coll. *Ziling*, comm. by K. E. Murashkinsky, B 0150. The specimen bearing this name was too badly eaten by insects for study.

POLYPORACEAE

Polystictus abietinus (Dicks.) Fr.

On *Abies sibirica*, District Sajany, Siberia, July, coll. *Murashkinsky.*

***Polystictus biformis** Klotzsch

On rotting wood of *Betula dahurica*, District Amur, Eastern Asia, August, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 089.

***Polystictus hirsutus** (Wulf.) Fr.

On *Prunus Padus*, District Tomsk, Siberia, August, coll. *Ziling*, comm. by K. E. Murashkinsky.

Polystictus pergamenus Fr.

On *Abies sibirica*, District Sajany, Siberia, August, coll. *Ziling*, comm. by K. E. Murashkinsky; on *Carpinus betulus*, Dagestan, Russia, May, coll. *Sheludjanova*, comm. by K. E. Murashkinsky.

Polystictus radiatus (Sow.) Fr.

On *Betula japonica*, District Amur, Eastern Asia, August, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 099.

***Polystictus vulpinus** Fr.

On *Populus tremula*, District Sajany, Siberia, July, coll. and det. by *Murashkinsky.*

***Polyporus adustus** Fr.

On *Polulus tremula*, District Sajany, Siberia, July, coll. *Murashkinsky*, B 23; on *Populus tremula*, District Tara, Siberia, October, coll. *Ziling;* on *Betula pubescens*, District Omsk, Siberia, August, coll. *Murashkinsky*, B 31; on *Carpinus cordata*, District Vladivostok, Eastern Asia, August, coll. *Ziling*, comm. by K. E. Murashkinsky, B 0151.

***Polyporus amorphus** Fr.

On *Pinus silvestris*, District Tara, Siberia, June, coll. *Murashkinsky*, B 2.

Polyporus benzoinus (Wahl.) Fr.

On *Picea excelsa*, District Tara, Siberia, September, coll. *Subatsh*, comm. by K. E. Murashkinsky, B 18.

***Polyporus brumalis** (Pers.) Fr.

On *Betula japonica*, District Amur, Eastern Asia, October, coll. *Krawtzew;* on *Betula dahurica*, Blagowietschensk, Eastern Asia,

October, coll. *Krawtzew*, both comm. by K. E. Murashkinsky, B 0102 and B 0104 respectively.

Polyporus delectans Pk.

On *Quercus mongolica*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 0126.

Polyporus dichrous Fr.

On *Betula pubescens*, District Sajany, Siberia, September, coll. *Konjev*, comm. by K. E. Murashkinsky, B 15; on *Populus tremula*, District Tara, Siberia, June, coll. *Murashkinsky*, B 50.

Polyporus dryadeus (Pers.) Fr.

On *Populus tremula*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 0100.

Polyporus fibrillosus Karst.

Polyporus aurantiacus Pk.

On *Picea excelsa* and on *Pinus silvestris*, District Sajany, Siberia, June, coll. *Murashkinsky*, B 6 and an unnumbered specimen.

Polyporus frondosus Fr.

On buried wood, District Amur, Eastern Asia, August, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 0201.

Polyporus gilvus Schw.

On *Quercus mongolica*, District Vladivostok, Eastern Asia, July, coll. *Ziling*, comm. by K. E. Murashkinsky, B 0132.

Polyporus hispidus (Bull.) Fr., resupinate.

On *Quercus mongolica*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 0124.

The fragment of a fructification received consists of resupinate tubes 15 mm. long, 3 to a mm., attached by a thin layer of substance to oblique surfaces of decorticated wood. No setae are present in the hymenium, spores are copious, colored, even, somewhat flattened on one side, $5\text{–}7 \times 4\text{–}5\ \mu$. The specimen is so similar to *P. hispidus* in tubes, color of substance, and in spores that it seems to be from a resupinate portion of *P. hispidus* on an oblique surface. Nevertheless it may be a true *Poria* of a species not known to me.

Polyporus lacteus Fr.

On *Populus tremula*, District Omsk, Siberia, October, coll. *Ziling;* on *Betula verrucosa*, District Tomsk, Siberia, August, coll. *Ziling;* on *Salix* sp., District Amur, Eastern Asia,—all comm. by K. E. Murashkinsky, B 14, an unnumbered specimen, and B 098.

Polyporus lentus Berk.

On *Betula pubescens*, District Omsk, Siberia, September, coll. *Ziling*, comm. by K. E. Murashkinsky, B 29.

Polyporus melanopus (Swartz) Fr.

On *Abies sibirica*, District Tara, Siberia, October, coll. *Baranov;* on *Abies sibirica*, District Sajany, coll. *Murashkinsky*, B 60.

Polyporus osseus Kalchb.

On *Betula verrucosa*, District Omsk, Siberia, August, coll. *Ziling*, comm. by K. E. Murashkinsky, B 19.

Polyporus pubescens (Schum.) Fr.

On *Quercus mongolica*, District Amur, Eastern Asia, August, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 0128.

Polyporus resinosus (Schrad.) Fr.

On *Abies sibirica*, Altai, Mongolia, July, coll. *Baranov*, comm. by K. E. Murashkinsky.

Usually found on wood of frondose species in collections by the writer.

Polyporus rutilans (Pers.) Fr.

On *Populus tremula*, District Tara, Siberia, July, coll. *Murashkinsky*, B 62.

Polyporus spumeus (Sow.) Fr.

On *Quercus mongolica*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 0130.

Polyporus squamosus (Huds.) Fr.

On *Populus tremula*, Altai, Mongolia, coll. *Shingosijev*, comm. by K. E. Murashkinsky.

Polyporus trichrous Berk. & Curtis?

On *Betula verrucosa*, Altai, Mongolia, August, coll. *Smirnov*, comm. by K. E. Murashkinsky, B 40.

Fructification is very thin, with soft, white substance sugges-

tive of *P. trichrous* and *P. leucospongia;* spores hyaline, even, 3–4 × 2–3 μ; no cystidia nor setae.

Fomes fulvus Fr.

On *Quercus mongolica,* District Amur, Eastern Asia, October, coll. *Krawtzew,* comm. by K. E. Murashkinsky, B 0127.

***Fomes igniarius** (L.) Fr.

On *Betula pubescens,* District Omsk, Siberia, June, coll. *Murashkinsky,* B 5; on *Betula verrucosa,* District Tara, Siberia, coll. *Murashkinsky;* on *Alnus fruticosa,* District Sajany, Siberia, coll. *Murashkinsky.*

***Fomes pinicola** Fr.

On *Picea excelsa,* District Tara, Siberia, July, coll. *Murashkinsky;* on *Pinus sibirica,* Tobolsk, Siberia, September, coll. *Dravert,* comm. by K. E. Murashkinsky; on *Abies sibirica,* Altai, Mongolia, July, coll. *Baranov,* comm. by K. E. Murashkinsky.

Fomes Palliseri Berk.

On *Picea excelsa,* District Tara, Siberia, August, coll. *Murashkinsky,* B 3.

Fomes roseus (Alb. & Schw.) Fr.

On *Abies sibirica,* District Sajany, Siberia, July, coll. *Murashkinsky.*

Trametes Abietis Karst.

On *Pinus silvestris,* District Tara, Siberia, coll. *Murashkinsky,* B 35.

Trametes hispida (Bagl.) Fr.

On *Populus nigra,* District Sajany, Siberia, June, coll. *Murashkinsky,* B 17.

Trametes inodora Fr. Icones Hym. *pl. 191, f. 1.*

On bark of decaying *Quercus mongolica,* District Amur, Eastern Asia, August 15 and 29, coll. *Krawtzew,* comm. by K. E. Murashkinsky, B 0121 and B 0125.

These specimens are referred to *Trametes inodora* rather than to *T. suaveolens,* because the tube mouths have not darkened and are rather regularly about 2 to a mm.

Trametes protracta Fr. Icones Hym. *pl. 191, f. 3.*

Trametes trabea Pers. sec. Bresadola, I. R. Accad. Agiati Atti III. **3**: 90. 1897.

On *Pinus silvestris*, District Barnaoul, Siberia, July, coll. *Konjev*, comm. by K. E. Murashkinsky, B 020; on *Populus tremula* and on *Quercus mongolica*, October and September, District Amur, Eastern Asia, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 090 and B 0105 respectively.

In one specimen there were found a few spores, colored, even, 10–11 × 7 μ, but so few that they may be foreign; all the specimens have cystidia with colored, capitate, aculeate tips.

Trametes radiata Burt, n. sp.

Type: in Burt Herb.

Fructification light drab of Ridgway, dimidiate, sessile, triquetrous, glabrous, strongly radiately rugose, the margin thin, entire; flesh white, soft, corky, equalling the tubes in thickness, drying without noteworthy taste or odor; tubes white, up to 8 mm. long, about 2–2½ to a mm., angular, the mouths warm buff, entire; no spores present; no cystidia, setae, nor hyphal fascicles present in the hymenium.

Fructification 4 cm. long, 7 cm. wide, 1½ cm. thick.

On *Betula dahurica*, District Amur, Eastern Asia, Oct. 15, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 0122.

Trametes radiata belongs in the group with *T. suaveolens* but has a smaller, light drab fructification which is strongly radiately rugose, and smaller tubes the mouths of which are not smoky.

Trametes suaveolens (L.) Fr.

On *Salix* sp., District Tara, Siberia, June, coll. *Murashkinsky*, B 10.

***Trametes stereoides** (Fr.) var. **Kmetii** Bres.

On *Salix* sp., District Omsk, Siberia, September, coll. *Ziling*, comm. by K. E. Murashkinsky.

***Trametes gibbosa** (Pers.) Fr.

On *Populus tremula*, District Tara, coll. *Murashkinsky*, B 21.

Daedalea confragosa (Bolt.) Fr.

On *Populus tremula*, District Tara, Siberia, August, coll. *Mu-*

rashkinsky, B 8; on *Betula verrucosa*, District Sajany, Siberia, September, coll. *Konjev*, comm. by K. E. Murashkinsky, B 11.

Daedalea aurea (Batt.) Fr.

On *Betula pubescens*, District Tara, Siberia, September, coll. *Murashkinsky*.

***Daedalea quercina** (L.) Fr.

On rotting trunks, District Vladivostok, Eastern Asia, June, coll. *Ziling*, comm. by K. E. Murashkinsky, B 0132.

Remarkable by having diameter of tubes and thickness of dissepiments only about half that of American and European specimens.

***Daedalea unicolor** (Bull.) Fr.

On *Betula pubescens*, District Omsk, and on *Betula verrucosa*, District Sajany, Siberia, September and July, coll. *Murashkinsky*, B 22 and an unnumbered specimen.

Poria caesio-alba Karst.

On *Abies holophylla*, Primorje, District Vladivostok, Eastern Asia, June, coll. *Ziling*, comm. by K. E. Murashkinsky, B 032c.

Poria laevigata Fr.

On *Betula pubescens*, District Omsk, Siberia, September, coll. *Ziling*, comm. by K. E. Murashkinsky, B 27.

Poria mucida (Pers.) Fr.

On bark of *Picea excelsa*, Altai, Mongolia, July, coll. *Murashkinsky*, B 33.

Poria taxicola (Pers.) Bres.

On *Pinus silvestris*, District Tara, Siberia, June, coll. *Murashkinsky*.

This specimen has hyaline, even, allantoid spores 4–4½ μ, not abundant; no setae, cystidia, hyphal fascicles, nor gloeocystidia.

Poria xantha Fr.

On charcoal, District Tara, Siberia, coll. *Murashkinsky*.

Porothelium Friesii Mont.

On *Abies sibirica*, District Tara, Siberia, September, coll. *Murashkinsky*, B 08.

Separable; spores colorless, even, 4 × 2½ μ; no setae, cystidia, nor hyphal fascicles.

Merulius serpens Fr.

On bark of *Juniperus communis*, District Tara, Siberia, June, coll. *Murashkinsky*.

***Merulius tremellosus** Fr.

On *Betula pubescens*, District Omsk, Siberia, September, coll. *Murashkinsky*, B 7 and an unnumbered specimen.

HYDNACEAE

Hydnum auriscalpium L.

On *Pinus silvestris*, District Omsk, Siberia, September, coll. *Baranov*, comm. by K. E. Murashkinsky.

Hydnum Erinaceus Bull.

On *Quercus mongolica*, District Amur, Eastern Asia, November, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 082.

Hydnum Hollii (Schmidt) Fr.

On rotting frondose wood, District Omsk, Siberia, September, coll. *Ziling*, comm. and det. by K. E. Murashkinsky.

Hydnum Murashkinskyi Burt, n. sp.

Type: in Burt Herb.

Fructifications coriaceous-corky, drying rigid, dimidiate, sessile, slightly decurrent at the base, imbricate, laterally confluent, concentrically sulcate, fibrillose, drying cinnamon-buff of Ridgway, the margin thin, light-colored, entire, substance up to 4 mm. thick, colored like the pileus; teeth snuff-brown, 2–4 mm. long, cylindric, acute, 240 μ in diameter, about 3–4 to a mm.; no special conducting organs in substance, trama, or hymenium; no cystidia, occasional hyphal fascicles protruding from the hymenium; spores white, even, 2½ × 1½ μ.

Fructifications 1½–2 cm. long, 2–6 cm. broad by confluence, 6–8 mm. thick.

On bark of decaying *Betula verrucosa*, District Tara, Siberia, September 1, 1928, coll. *Murashkinsky*, B 04, type.

This species is related to *H. adustum* but the pileus is concentrically sulcate and glabrous, attached by the full width of the

dimidiate pileus rather than by a distinct stem or more or less stem-like base, and the hyphal fascicles of the hymenium are more conspicuous than those of *H. adustum.*

Hydnum ochraceum Pers.

On *Betula pubescens*, District Omsk, Siberia, July and September, coll. *Murashkinsky*, B 28 and an unnumbered specimen; on *Betula verrucosa*, District Tara, September, coll. *Murashkinsky*, B 010.

Hydnum reflexum Burt, n. sp.

Type: in Burt Herb.

Fructification 2½ cm. long, 4 cm. broad, effuso-reflexed, mostly resupinate, with the margin reflexed 5 mm., coriaceous, tomentose, drying cinnamon-buff of Ridgway, thin, entire; substance colored like reflexed surface, up to 1 mm. thick; teeth drying cinnamon, about 2 mm. long, cylindric, acute, about 3 to a mm.; no special conducting organs in the substance or the hymenium; no cystidia; small hyphal fascicles protrude from the hymenium up to 20 to 25 μ above its surface; a few floating spores are colorless, even, $4 \times 2\frac{1}{2}$ μ but may be foreign.

On bark of *Betula*, District Bijsk, Siberia, October 3, 1928, coll. *Dravert*, comm. by K. E. Murashkinsky, B 0129, type.

Hydnum reflexum may be distinguished from the effuso-reflexed species heretofore known by the tomentose, cinnamon-buff surface of the free margin, by the somewhat darker teeth, by the occurrence of hyphal fascicles like those of *Polyporus hirsutus* protruding here and there in the hymenium, and by the absence of cystidia.

Hydnum velutinum Fr.

On the ground, District Tara, Siberia, July, coll. *Murashkinsky.*

***Irpex fusco-violaceus** Fr.

On *Abies excelsa*, District Sajany, Siberia, September, coll. *Autonov,* comm. by K. E. Murashkinsky.

***Irpex lacteus** Fr.

On *Salix* sp., District Omsk, Siberia, September, coll. *Murashkinsky;* on *Betula verrucosa* and *Betula pubescens*, District Sajany, Siberia, July and August, coll. *Ziling,* comm. by K. E. Murashkinsky, B 16 and B 30 respectively.

Irpex pachyodon (Pers.) Bres.

On *Alnus hirsuta*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 0120.

Phlebia radiata Fr.

On *Betula verrucosa*, District Omsk, Siberia, August, coll. *Murashkinsky*, B 1.

Phlebia strigoso-zonata (Schw.) Lloyd. See Burt, Mo. Bot. Gard. Ann. **8**: 393–395. 1921.

On *Populus tremula*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 081.

Odontia bicolor (Alb. & Schw.) Bres.

On *Betula* sp., District Lushsk, Province Petrograd, August, coll. *Boudartzev*, comm. by K. E. Murashkinsky.

Kneiffia setigera Fr.

On *Alnus fruticosus*, District Sajany, July, coll. *Murashkinsky*, det. Kurpowa.

THELEPHORACEAE

***Craterellus cornucopioides** Fr.

On ground, District Irkutsk, Siberia, August, comm. by K. E. *Murashkinsky*.

Thelephora palmata (Scop.) Fr.

On ground, District Tara, Siberia, August 21, coll. *Murashkinsky*, B 06.

Thelephora tenuis Burt, n. sp.

Type: in Burt Herb.

Fructifications drying Verona brown of Ridgway, cespitose, dimidiate, sessile, imbricate, confluent, soft, flexible, fibrous, with the fibrils somewhat matted together to form a roughened but not squamulose upper surface, very thin, only 700 μ thick in section, the margin thin, concolorous; hymenium inferior, Verona brown, fibrous, even, not at all papillose; spores dark umbrinous under the microscope, subangularly globose or ellipsoidal, rough, 7–8 × 6–7 μ.

Clusters 3–4 cm. in diameter; individual pileus 1–1⅓ cm. long, 1½–2 cm. broad, 600–700 μ thick.

On sandy ground, District Amur, Eastern Asia, August 20, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 084, type.

Thelephora tenuis is related to *T. intybacea* but is thinner, with fibrils of the upper surface not matted into squamules, the margin concolorous, and the hymenium not papillose.

Thelephora terrestris Ehrh.

On ground, District Tara, Siberia, June, coll. *Murashkinsky;* on ground and on roots of *Quercus mongolica*, District Amur, Eastern Asia, July 27, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 096.

Hypochnus spongiosus (Schw.) Burt

On decaying wood of *Pinus silvestris*, District Tara, Siberia, September, coll. *Murashkinsky*, B 02.

Hypochnus umbrinus Fr. ?

On fallen limb of *Picea obovata*, District Tara, Siberia, August, coll. *Murashkinsky*, B 011.

Young, sterile, mycelial stage of this species in my opinion.

Stereum Chailletii Pers.

On *Pinus silvestris*, District Omsk, Siberia, September, coll. *Murashkinsky*.

Stereum fasciatum Schw.

On *Pinus* sp., District Tara, Siberia, September, coll. *Baranov;* on *Betula verrucosa* and on *Pinus silvestris*, District Barnaoul, Siberia, May, coll. *Konjev*, comm. by K. E. Murashkinsky, B 026 and B 027; on *Quercus mongolica*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 085 and B 0200; on deciduous wood, Primorje, District Vladivostok, Eastern Asia, June, coll. *Ziling*, comm. by K. E. Murashkinsky, B 037.

Stereum fasciatum is widely distributed; very common in North America, it is present in Herb. E. Fries at Upsala from Norway as the type of *Stereum arcticum*. I have two collections of *S. fasciatum* from the Tirol comm. by Litschauer under the name *S. lobatum*—a species of more tropical range. *S. fasciatum* is perhaps common in the southern hemisphere also, for I have received five collections from Professor P. A. van der Bijl made by him on

Eucalyptus and other wood at Victoria Falls, Rhodesia, Transvaal, and Cape, South Africa.

Stereum fuscum (Schrad.) Quelet (= *S. bicolor* Fr.)

On *Betula pubescens*, District Omsk, Siberia, September, coll. *Murashkinsky*, also *Ziling*, comm. by K. E. Murashkinsky, B 15; resupinate on *Quercus mongolica*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 080.

Stereum gausapatum Fr.

On *Quercus pedunculata*, Sestrorjetzk, Siberia, August, coll. *A. Boudartzev*, comm. by K. E. Murashkinsky.

Stereum hirsutum (Willd.) Fr.

On *Alnus fruticosus*, District Sajany, Siberia, July, coll. *Murashkinsky;* on *Betula verrucosa*, District Tara, Siberia, September, coll. *Murashkinsky*, B 096.

Stereum ochroleucum Fr.

On decaying limb of *Quercus mongolica*, District Amur, Eastern Asia, August 25, 1928, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 086.

This gathering is a very important find, for European mycologists since the time of Fries have erroneously referred to *S. ochroleucum* specimens of very different structure from that of the authentic specimen in Kew Herbarium, the true structure of which was given in detail in my work on *Stereum* in Mo. Bot. Gard. Ann. 7: 235. 1920.

In the present gathering from Eastern Asia the fructifications are smaller than the authentic specimen, for some of those wholly resupinate are only 2 mm. in diameter, whereas the larger narrowly reflexed specimens are about 5 mm. in diameter. The color and internal structure agree with those of the authentic specimen. The hyphae are interwoven throughout, 2½ μ in diameter, nodose-septate, with no intermediate layer of longitudinally arranged hyphae. No hardened crust nor golden zone marks the upper limit of the intermediate layer. No gloeocystidia nor colored conducting organs are present. The spores are copious for a *Stereum*, hyaline, even, $4\frac{1}{2}$–$6 \times 3\frac{1}{2}$–4 μ.

Since known stations for *S. ochroleucum* are Sweden and Amur, future collections may be expected from Russia and Siberia.

Stereum Pini Fr.

On *Pinus silvestris,* District Barnaoul, Siberia, July, coll. *Konjev,* comm. by K. E. Murashkinsky, B 018.

***Stereum rhytidocyclum** Sacc. & F. Sacc. Soc. Roy. Bot. Belg. Bul. **28:** 79. *pl. 4. f. 1.* 1889; Syll. Fung. **9:** 226. 1891.

On wood which has microscopic structure of a frondose species but is erroneously stated on the label as *Abies sibirica,* District Tara, Siberia, August, coll. *Murashkinsky,* B 05. The type was collected on trunks of *Sorbus Aucuparia* in subalpine woods, Golubaja, Siberia.

The present Tara gathering is effuso-reflexed with the resupinate part about 3–5 × 1½–2 cm. and one margin reflexed about 2–3 mm., concentrically sulcate on the upper surface, warm buff of Ridgway and rough but not hairy, the margin entire; hymenium even, cinnamon-drab of Ridgway; in section about 700 μ thick, composed of loosely arranged, colorless, even-walled, rather rigid, somewhat interwoven hyphae not nodose septate, 2–3 μ in diameter, which extend obliquely from substratum to hymenium and have their tips somewhat colored and agglutinate in the hymenium; no colored conducting organs, setae, cystidia, nor hyphal fascicles; the only spore found is colorless, even, about 14 × 8 μ but may be foreign.

This species may be distinguished from *Stereum sanguinolentum* by absence of colored conducting organs and occurrence on frondose wood, and from *S. fasciatum* and *S. hirsutum* by more paper-like consistency and upper surface of reflexed margin not being tomentose nor hirsute.

Stereum rugosiusculum Berk. & Curtis. See Burt, Mo. Bot. Gard. Ann. **7:** 127. *text f. 14.* 1920.

On *Populus tremula,* District Tara, Siberia, August, coll. *Murashkinsky,* B 07 and B 013.

Stereum rugosum Pers.

On *Alnus fruticosa,* District Sajany, Siberia, July, coll. *Murashkinsky.*

Stereum sanguinolentum Alb. & Schw.

On *Pinus silvestris,* District Tara, Siberia, August and September, coll. *Ziling,* 2 unnumbered specimens comm. by Murashkin-

sky; on *Picea excelsa* and *Abies sibirica*, District Tara, Siberia, September, coll. *Murashkinsky*, B 09a and B 014.

Stereum spadiceum (Pers.) Bres.
On *Ailanthus glandulosa*, Russia, July, ex Herb. Jaczewski, comm. by K. E. Murashkinsky.

Stereum sulcatum Burt
On *Larix sibirica*, Altai, Mongolia, July, coll. *Murashkinsky*, comm. as *S. Karstenii* Bres.; on living aged trunk of *Chamaecyparis formosensis*, altitude 6000–8000 ft., Formosa, Japan, comm. by D. Numata, Kyoto Imperial Univ.

Stereum versiforme Berk. & Curtis
On *Quercus mongolica* and *Rhododendron* sp., District Amur, Eastern Asia, August to October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 083, B 087, and B 0131 respectively.

Hymenochaete badio-ferruginea (Mont.) Lév.
On *Larix dahurica*, District Amur, Eastern Asia, August, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 0101.

Hymenochaete Mougeotii (Fr.) Cooke
On *Rhododendron dahurica*, District Sajany, Siberia, July, coll. *Murashkinsky;* on *Abies sibirica*, District Tara, October, coll. *Sheludjakova*, comm. by K. E. Murashkinsky.

***Hymenochaete tabacina** (Sow.) Lév.
On *Prunus Padus*, District Tara, Siberia, October, coll. *Baranov*, comm. by K. E. Murashkinsky.

Corticium confluens Fr.
On *Quercus mongolica*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 092.

Corticium frustulosum Bres.
On *Pinus silvestris*, District Tara, Siberia, August, coll. *Murashkinsky*, B 03.

Corticium galactinum Fr.
On *Quercus mongolica*, District Amur, Eastern Asia, September, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 0103.
In Mo. Bot. Gard. Ann. **13**: 202. 1926, I reported specimens of

this species from Japan, Prov. Awaji, collected by Yasuda at Hiroto-Mura and Mt. Mikuma.

Corticium hydnans (Schw.) Burt

Corticium colliculosum Berk. & Curtis; *C. Queletii* Bres.

On *Salix* sp., District Barnaoul, Siberia, June, coll. *Konjev*, comm. by K. E. Murashkinsky, B 025.

Corticium illaqueatum Bourd. & Galz.

On charred wood of *Populus tremula*, District Barnaoul, Siberia, May, coll. *Konjev*, comm. by K. E. Murashkinsky, B 029.

Corticium investiens (Schw.) Bres.

On *Pinus silvestris*, District Tara, Siberia, September, coll. *Murashkinsky*, B 012.

Corticium lactescens Berk.

On *Salix* sp., District Omsk, Siberia, September, coll. *Murashkinsky.*

Corticium laeve Pers.

On *Abies sibirica*, District Wjatka, April, coll. *Fokia*, comm. by K. E. Murashkinsky.

Corticium ochraceum Fr.

On *Sorbus Aucuparia*, District Sajany, Siberia, July, coll. *Ziling*, comm. by K. E. Murashkinsky.

Corticium polygonium Pers.

On fallen twig of *Populus* sp., District Sajany, Siberia, July, coll. *Murashkinsky.*

Corticium radiosum Fr.

On *Pinus silvestris*, District Tara, Siberia, August, coll. *Murashkinsky.*

Corticium roseum Pers.

On *Salix* sp., District Tara, Siberia, June, coll. *Murashkinsky.*

Corticium sulphureum Fr.

Young, sterile mycelial stage on *Philadelphus* sp., Promorje, District Vladivostok, Eastern Asia, July, coll. *Ziling*, comm. by K. E. Murashkinsky, B 035.

Peniophora corticalis (Bull.) Bres. (= *Peniophora quercina* (Pers.) Cooke).

On *Quercus mongolica*, District Amur, Eastern Asia, November, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 091.

Peniophora gigantea (Fr.) Massee

On *Pinus silvestris*, District Tara, Siberia, August, coll. *Murashkinsky.*

Peniophora mutata (Peck) Bres.

On *Populus tremula*, District Sajany, Siberia, July, coll. *Murashkinsky;* on *Populus tremula*, District Tara, Siberia, coll. *Poljakov*, comm. by K. E. Murashkinsky.

Coniophora byssoidea (Pers.) Fr.

On wood of *Pinus silvestris*, District Barnaoul, Siberia, June, coll. *Konjev*, comm. by K. E. Murashkinsky, B 028.

Coniophora olivacea (Fr.) Karst.

On charred wood of *Pinus silvestris*, District Barnaoul, Siberia, May, coll. *Konjev*, comm. by K. E. Murashkinsky, B 030.

Coniophora sibirica Burt, n. sp.

Type: in Burt Herb.

Fructification effused, membranaceous, separable when moistened, fibrous, drying raw umber of Ridgway, the margin thinning out, concolorous; hymenium even, pulverulent, not setulose; structure in section 200–250 μ thick, composed of loosely interwoven, rigid, even-walled, non-incrusted, dark-colored hyphae 4–5 μ in diameter, which give their color to the fructification and are not nodose-septate; no cystidia; spores colored, even, 11 × 6 μ.

On decaying coniferous wood, probably *Pinus silvestris*, District Tara, Siberia, August, 1921, coll. *Murashkinsky*, comm. as *C. atrocinerea.*

Coniophora sibirica is related to *C. arida* but is distinct by coarser, thicker-walled, and more rigid hyphae and fructifications which may be peeled away from the substratum when moistened.

Aleurodiscus disciformis (DC.) Pat.

On bark of *Acer* sp., Primorje, District Vladivostok, Eastern Asia, June, coll. *Ziling*, comm. by K. E. Murashkinsky, B 033.

***Aleurodiscus diffissus** (Sacc.) Burt, n. comb.

Peniophora diffissa Sacc. Soc. Roy. Bot. Belg. Bul. **28**: 79. *pl. 4. f. 2.* 1889; Syll. Fung. **9**: 239. 1891.

Fructifications gregarious, crowded, somewhat disk-shaped, tuberculiform, wood-brown of Ridgway, cracking to the substratum and splitting into small fructifications, coriaceous, centrally attached, the margin free, darker underneath; hymenium wood-brown, coarsely wrinkled, not shining; in section 500 μ thick, army-brown, composed of suberect, interwoven, colored hyphae about 2 μ in diameter, with a darker zone along the substratum; bottle-brush paraphyses (dendrophyses) with deeply staining body about 4 μ in diameter, and numerous slender lateral branches about 4 μ long are intermixed with other infrequent paraphyses having somewhat moniliform tips; spores hyaline, even, globose, 5½–6 μ in diameter.

On bark of decaying *Rhododendron dahuricum*, District Sajany, Siberia, July 11, 1927, coll. *Murashkinsky*.

Aleurodiscus diffissus resembles somewhat in aspect *Stereum rufum* and *Corticium polygonium*. The small fructifications 1–2 mm. in diameter and 500 μ thick are densely gregarious over areas up to 5 cm. long by 2 cm. wide and show well the character of forming new fructifications by splitting, as shown by Saccardo in his fig. 2b and upon which he based the specific name. The hymenial bottle-brush and moniliform paraphyses are like those of *A. cerrusatus*.

Cytidia salicina (Fr.) Burt

On *Salix* sp., District Tara, Siberia, September, coll. *Ziling*, comm. by K. E. Murashkinsky.

Microstroma Juglandis Sacc.

On living leaves of *Juglans regia*, Russia, July, comm. by K. E. Murashkinsky.

This species is included by some authors in the Basidiomycetes.

CLAVARIACEAE

Clavaria formosa (Pers.) Fr.

On the ground, District Amur, Eastern Asia, August, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 088.

DACRYOMYCETACEAE

Ditiola conformis Karst.

On rotting coniferous wood, District Tara, Siberia, October, coll. *Baranov*, comm. by K. E. Murashkinsky.

Femsjonia luteo-alba Fr.

On *Pinus silvestris*, District Barnaoul, Siberia, August, coll. *Konjev*, comm. by K. E. Murashkinsky, B 019.

TREMELLACEAE

***Exidia glandulosa** (Bull.) Fr.

On *Betula verrucosa*, District Omsk, Siberia, August, coll. *Murashkinsky.*

Eichleriella spinulosa (Berk. & Curtis) Burt

On *Populus nigra*, District Sajany, Siberia, coll. *Katajewskaja*, comm. by K. E. Murashkinsky.

Sebacina calcea (Pers.) Bres.

On *Larix sibirica*, District Sajany, Siberia, July, coll. *Murashkinsky.*

AURICULARIACEAE

Auricularia auricula-Judae (L.) Schroet.

On *Ulmus* sp., Prov. Primorsk, Eastern Asia, July, coll. *Avotia*, comm. by K. E. Murashkinsky, B 45.

Auricularia auriformis (Schw.) Earle

On *Quercus mongolica*, District Amur, Eastern Asia, October, coll. *Krawtzew*, comm. by K. E. Murashkinsky, B 095.

The specimen, somewhat shattered in transit, is dark mouse-gray and somewhat olivaceous where hairs are best developed, 2½ cm. broad, very thin, 1260 μ in section, with hairs of the upper surface 40–60 μ long, not at all bulbous at base; spores 9–16 $\times$ 4–5μ. The specimen agrees well with gatherings from South Carolina in my herbarium which I compared with an authentic specimen from Herb. Schweinitz.

Septobasidium Carestianum Bres.

On *Ribes* sp., District Sajany, Siberia, July, coll. *Murashkinsky.*

Annals of the Missouri Botanical Garden

Vol. 18 NOVEMBER, 1931 No. 4

THE EFFECT OF MONOCHROMATIC ULTRA-VIOLET LIGHT OF MEASURED INTENSITIES ON BEHAVIOR OF PLANT CELLS[1]

PRELIMINARY REPORT

ALEXANDER F. BUCHOLTZ

Formerly Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany of Washington University
Formerly Assistant in Botany, Henry Shaw School of Botany of Washington University

Introduction and Discussion of Previous Work

The effect of ultra-violet radiation on plants has been the subject of numerous investigations, but most of the results obtained are either indefinite or contradictory. Hardly anything is yet known about the physical and chemical reactions involved. To make any progress in this direction, that is, to seek a physical and chemical explanation for the action of ultra-violet radiation on living cells, it would be essential to accumulate exact quantitative data on the subject. The lack of quantitative measurements of the spectral qualities of the source of radiation is notably the weakest point in most of the investigations, and therefore it becomes almost impossible to correlate or interpret the results obtained.

According to the fundamental law of photochemistry (Grotthuss-Draper Photochemical Absorption Law) only rays which are absorbed are effective in producing chemical changes. However, not all absorbed energy has to result in chemical reactions,

[1] An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

since radiation may be transformed into another form of radiant energy or produce a change in the energy content of the molecule. According to Einstein's concept of quantum absorption, the occurrence of photochemical reactions is due to the absorption of quanta of radiation, each single molecule requiring one quantum of a frequency characteristic of the absorbing molecule. This concept, based on parallelism with the photoelectric effect, indicates a more or less specific action of different quanta. A quantum of a given energy value can be expressed as a particular frequency or wave length. Of course, one should not forget that the absorption of radiant energy by a molecule is much more complex than it is in an atom and that Einstein's concept applies only to the primary stage of a photochemical reaction. Secondary chemical processes initiated by the primary stage will often be entirely independent from the light action.

It is clear, however, that the use of monochromatic light will help to explain many of the essential factors in photochemical and photobiological investigations.

The necessity of confining one's self to the study of the action of narrow spectral regions in the ultra-violet becomes especially clear if one considers the nature of absorption bands in this part of the spectrum. Ribaud ('13), who studied and compared absorption bands of different gases, liquids, and solids in different spectral regions, came to the conclusion that the width of the absorption bands decreases continuously on going from the infra-red toward the ultra-violet end of the spectrum and is nearly proportional to the wave-length maximum. It is also clear that as long as the absorption of radiant energy involves a given quantum per absorbing molecule the number of quanta or the intensity of absorbed radiant energy must be determined. The Bunsen-Roscoe reciprocity law of photochemistry states that when the product of intensity and exposure time is constant a constant photochemical reaction results. With some modifications the law holds for most of the chemical compounds tested.

As far as the biological action of radiant energy is concerned, there is no reason to believe that the laws of photochemistry are not applicable, even though the situation be much more

complex. As a matter of fact, several of the photochemical laws have been tested for biological objects. The correlation between the absorption spectrum of chlorophyll and the rate at which carbon dioxide is decomposed by the plant was studied as early as 1875 by Timiriazev ('75). Gates ('30), using accurate quantitative measurements, found that the absorption curve of bacteria corresponded strikingly to the curve obtained for the lethal action of different wave lengths and intensities of the incident energy.

Verhoeff and Bell ('16), in their investigations on the harmful effect of ultra-violet radiation on the cornea of the eye, found that the time of exposure necessary to produce symptoms of injury is inversely proportional to the intensity of radiation of the effective ray. Similar results were obtained by Hill and Eidenow ('23) and Weinstein ('30) with paramecia, and Barr and Bovie ('23) with amoebae. Coblentz and Fulton ('24) emphasized the fact that longer exposures do not fully compensate for decreased intensity. An intensity reduction to 1/50 required an increase of $\times$ 75 in the exposure time to produce a comparable reaction on bacteria. Gates ('29a) tested the validity of this Bunsen-Roscoe law by the killing effect of ultra-violet radiation on bacteria. He worked with monochromatic light and, measuring intensities by means of a sensitive thermopile, found that the law does not hold strictly, especially with young and metabolically and genetically active bacteria, although it is fairly accurate if small differences in intensities are used.

The results obtained by Verhoeff and Bell ('16), Bovie ('16), Barr and Bovie ('23), and Weinstein ('30) indicate that within certain limits, the same total exposure is required to produce the effect when the radiation is interrupted for short intervals as when it is continuous.

In the light of the preceding discussion it becomes evident that the quality and quantity of light play important parts in the effect it will produce on living matter.

The literature on the action of ultra-violet radiation on plants has been reviewed by Eltinge ('28), Arthur and Newell ('29), and Fuller ('31). As emphasized by Fuller, the fact that sources of radiation of unknown spectral quality have been used in

most investigations makes it almost impossible to compare the results obtained by various workers. He also emphasized the fact that in biological effects radiation from artificial sources of light, such as mercury vapor arcs, can by no means be compared with the radiation of the sun.

To eliminate some of the uncertainty about the spectral aspects of the source of radiation, a number of workers have used filters of various makes to limit the radiation to certain parts of the spectrum. However, unless spectrographs of the transmission of light through the filter are given one cannot be certain about the quality of the spectrum, since commercial mercury vapor arcs vary in this respect according to make, the length of time they have been used, etc. Furthermore, the use of selective filters introduces a number of complications due to the partial absorption of spectral lines other than those eliminated. The relative intensities of the different parts of the spectrum are thus distorted, and one does not know whether the effect produced by interposing a filter is due to the elimination of a certain spectral region or to the weakening of the intensity of the wave lengths transmitted. Besides, spectrographs are usually taken by interposing the filter between the spectroscope and the source of light placed close to the filter, while the objects during irradiation are placed at quite a distance from the source, sometimes as much as 100 inches. Henri (cited by Taylor, '31) claimed to have shown that a strict relationship exists between the infra-red and ultra-violet in their photochemical action. Reiter and Garbor ('28) claimed to have established an antagonistic relationship between the action of two different bands in the ultra-violet spectrum on cell division.

The only way then to get a clear picture of the action of ultra-violet light on organisms would be to use monochromatic light of measured intensities, so that the actual energy falling on the object under investigation could be definitely determined. It is true that monochromatic light does not occur in the natural surroundings of the plant, and therefore cannot be regarded as a normal environmental factor. However, the selective absorption of light by the organic substances of the plant and the fact that it affords the only accurate means of determining the

quantity and quality of light make it advisable to investigate, first, the biological action of monochromatic light and, later on, to synthesize the results.

Several investigators have exposed their objects to radiation passed through a quartz spectrograph. Ward ('93) was the first to use this method for the study of the bactericidal action of light. He was followed by a number of workers.

Hertel ('05) seems to be the first who fully recognized the importance of quantitative measurements of the intensities of monochromatic light used for biological studies. Using a quartz prism and lenses, he constructed a monochromator similar to those used in ultra-violet microscopy. He determined the relative intensities of the lines by means of a thermopile and varied the intensity by regulating the amperage of the metallic arc. He used four lines of the ultra-violet part of the spectrum and studied their effects on paramecia, diatoms, *Oscillaria*, and *Elodea*. He found that the line 2800 Å was the most powerful in its destructive action on cells, and noticed that not only was the streaming in the cells of *Elodea* retarded by the light but also that the cells finally died.

Schulze ('09) devoted himself to the study of the effect of the powerful line of 2800 Å of the magnesium spark. As objects he used cells of *Spirogyra, Nitella, Vallisneria,* and *Elodea,* root hairs of *Hydrocharis,* anther hairs of *Tradescantia,* and hyphae of *Mucor.* He employed a monochromator similar to that used by Hertel and focused the rays by means of quartz lenses on the stage of the microscope. The intensity was varied by means of regulating the amperage across a magnesium spark. He found that at certain intensities small vacuoles appear in the cells, that protoplasmic streaming is retarded, and that longer exposures result in death of the cells. The growth of hyphae of *Mucor* and the cell division in *Tradescantia* were retarded. Even when using relatively small intensities he was unable to detect stimulation. By means of microphotographs he showed that the cuticle and epidermis strongly absorb the ultra-violet of this frequency. Parenchyma tissue, phloem, and young cambium were quite transparent to the light, whereas xylem again absorbed it rather strongly. As far as the different parts of the cell were

concerned, he showed that the strongest absorption was in the middle lamella. Strong absorption was also shown by the nuclei and chromosomes. Unfortunately it is impossible to ascertain the exact intensities used in his experiments.

Frank and Gurwitsch ('27), in trying to discover the cause of the so-called mitogenetic radiation which they claimed is emitted by embryonic tissue, used a small quartz spectrograph to determine the physical nature of the radiation. They believed that the wave lengths of 1930–2370 Å at one-minute exposure produced a stimulating effect on the cell division of the root of the onion similar to that produced by mitogenetic rays.

Reiter and Garbor ('28), in their extensive study on mitogenetic rays, employed a specially constructed spectrograph which permitted them to combine at one focal point several wave lengths. By using a number of arcs and sparks to obtain a large number of lines in the ultra-violet part of the spectrum, they found that the line 3400 Å, and to a lesser degree, line 2800 Å produce a stimulating effect on cell division in the root of the onion, eggs and larvae of the frog and salamander, and sarcoma tissue of the rat. This was evident only at relatively low intensities, whereas at higher intensities the same rays were destructive. If the spectral region of 2900–3200 Å was added to the radiation of the line 3400 Å, the stimulating as well as destructive action of the radiation disappeared. Frank ('29) disagreed with Reiter and Garbor as to the wave length involved in mitogenetic radiation. In rechecking his earlier observations he found that the spectral region between 2000 and 2400 Å is effective. He even claims to have obtained a mitogenetic stimulation of yeast in this region by passing the radiation from that of a biological source through a powerful quartz spectrograph. Neither Reiter and Garbor nor Frank gave the measurements for the intensities employed.

Recently Gates ('29a, '29b, '30) published a series of investigations on the bactericidal action of ultra-violet light. Using monochromatic light from a specially constructed powerful monochromator and measuring the intensity of the incident radiation in absolute energy units by means of a thermopile, he studied the lethal effects of ten lines of the mercury vapor

spectrum on *Bacillus coli, B. communis,* and *Staphylococcus aureus.* These papers have probably contributed more to the clarifying of the topic under discussion than all the rest of the investigations taken together and demonstrated the value of the use of monochromatic light of measured intensities in the study of biological objects. In the first paper of the series Gates determined the curves of bactericidal action for each wave length studied. He found that with all the different wave lengths the reactions followed similar curves, but occurred, at each wave length, at a different energy level. In his second paper he studied the effect of various environmental factors on the bactericidal action of ultra-violet and determined the wave length limits of the action as being between 3130 and 2250 Å, although the lower limit could not be definitely ascertained. In the third paper the absorption curves of the body of the bacteria were determined and correlated with the curve of incident energy instrumental in the bactericidal action. Although some minor differences are evident in the curves, they form in general a reciprocal of each other. He proved that the belief that the shorter the wave-length the greater the bactericidal action of ultra-violet is erroneous, and that a striking maximum of effectiveness exists between 2600 and 2700 Å. Having thus accumulated quantitative data on the subject, he promises a discussion of the photochemical action of the radiation in his next paper.

Weinstein ('30), also using similar quantitative measurements and focusing monochromatic light on the stage of a microscope, made observations of the effect of five wave lengths of the ultra-violet part of the spectrum on *Paramecium micromultinucleatum.* The line of 2650 Å was found to be most effective in killing paramecia.

Marshall and Knudson ('30), by means of similar methods, studied the effect of monochromatic light on the formation of vitamin D from ergosterol. They found that the rate of production of the vitamin is directly proportional to the number of light quanta absorbed by ergosterol. The reaction was found to be independent of the wave length within the absorption region of ergosterol.

Apparatus Used

To be able to obtain quantitative data on the action of ultra-violet radiation on plant cells a Bausch and Lomb quartz mono-chromator was used. The instrument is of the constant deviation type and calibrated for the wave lengths from 2000 to 8000 Å. The intensity of the radiation was measured by means of a Coblentz bismuth-silver thermopile adapted by the B. & L. Optical Company for their monochromator. The thermopile is mounted on an adapter in such a manner that it can be lowered in front of the slit when intensity measurements are taken and raised above the slit to permit the light to pass into the space. The relative positions of the thermopile (b) in its adapter (c) can be seen by comparing figs. 1 and 3, pl. 42. The metal box containing the thermopile and supplied with a quartz window was sealed air-tight and evacuated through an outlet (d). It was found that, although it was difficult to maintain a high vacuum for long periods, one could get a relatively constant partial vacuum by evacuating the box while measurements were taken. An oil vacuum pump was used for evacuation.

The thermopile was connected with a Type HS Leeds and Northrup galvanometer having a sensitivity of 20 mm. per μv. and an internal resistance of 16.8 ohms. Since the resistance of the thermopile was found to be equal to the critical damping resistance of the galvanometer (7.5 ohms) no additional resistances were placed in the circuit. The deflections were read through a telescope at 2 meters scale distance.

The thermopile was calibrated in absolute energy units (mechanical equivalent) against a Bureau of Standards carbon filament incandescent lamp No. C-109. The reaction of the thermopile was found to be linear, and a 1 mm. deflection on the galvanometer corresponded to a light energy of 7.22 erg/mm.^{2}/second. The readings of the intensity of the different spectral lines taken at various times were quite constant, varying within the limit of 5 per cent.

As a source of light, at first a horizontal air-cooled quartz mercury vapor arc of the Burdick Cabinet Company was tried but proved to be of insufficient intensity for monochromatic work. A vertical water-cooled Burdick arc (type W-910) operated

at 55 volts and 4.3 amperes was used in most of the experiments. It was placed at a distance of 4 cm. from the entrance slit of the monochromator. This lamp is supplied with a filter of water 1 cm. deep, so that most of the infra-red radiation is probably eliminated.

The distribution of the spectral lines in the ultra-violet region and their relative intensities as measured by the thermopile are represented in fig. 1.

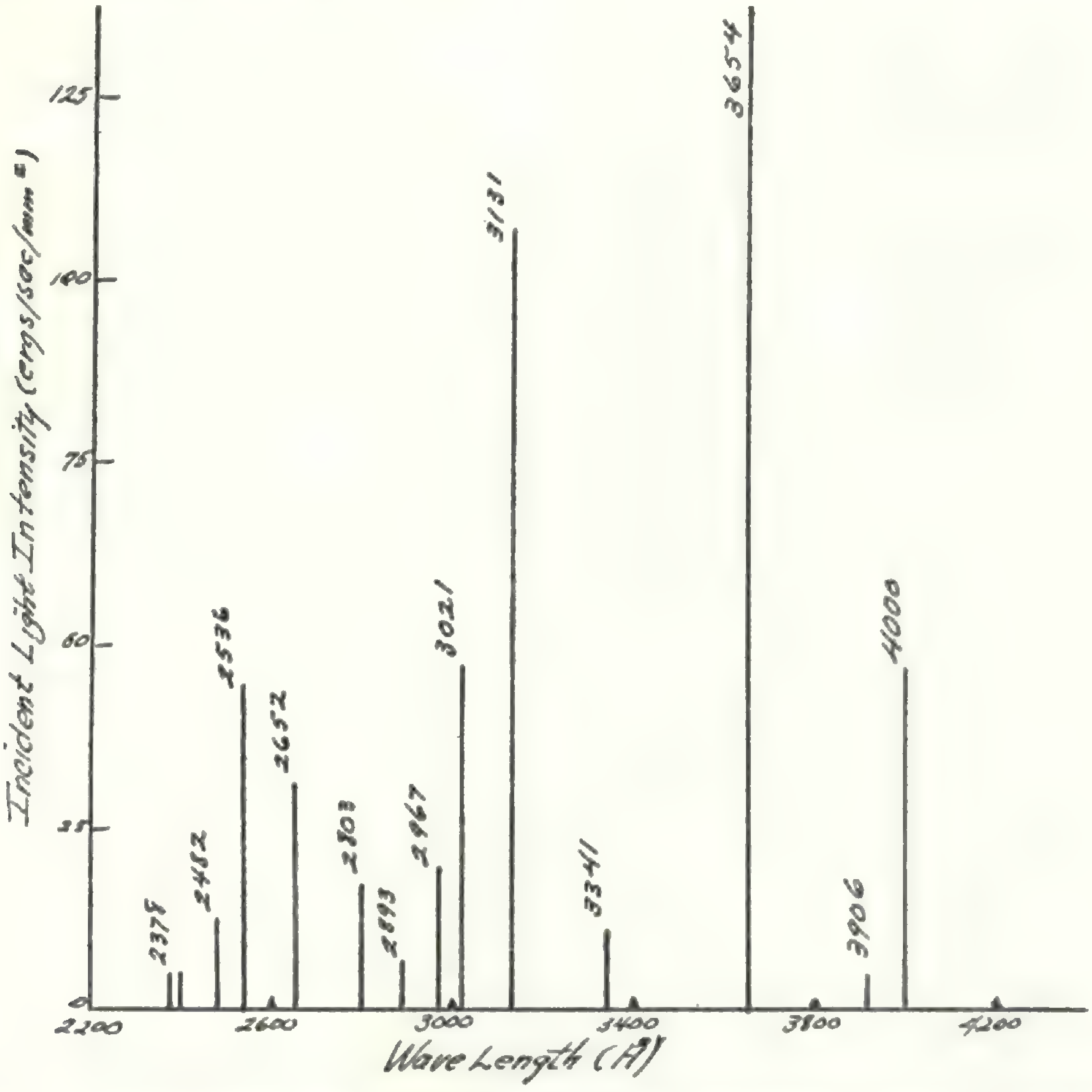


Fig. 1. Distribution and relative intensities of the spectral lines of a Burdick water-cooled mercury arc.

The widths of the entrance and exit slits of the monochromator were kept constant at 0.2 mm., representing an area of 2 mm.[2]

Considerable difficulties were experienced in so adjusting the objects studied that they could be examined by a microscope and the incident energy could be determined by the thermopile. Even at a distance of 1 cm. from the exit slit of the monochro-

mator the rays are dispersed to a considerable extent. As illustrated in pl. 42, figs. 1 and 2, a metallic tube (e) supported by an adjustable stand (g) was placed in the path of the ray passing from the monochromator (j). By means of a quartz lens (f) the image of the exit slit of the monochromator was reproduced on a second slit just behind the thermopile (b). One end of the tube was shaped in such a manner that the whole thermopile adapter (c), including the thermopile and the adjustable slit, could be removed during the raying and slipped into position during intensity measurements.

Plate 42, fig. 2, shows the set-up during the raying. A vertical adjustable microscope stage (h) supporting a slide with the object (i) under investigation was placed in front of the tube. In this way the image of the exit slit of the monochromator was focused on the subject. The observations were made, and the focusing of the ray was done by means of a horizontal microscope (a). For microscopic examination of the objects during the experiments a micro-lamp was interposed between the lens (f) and the monochromator (j). Since the quartz lens absorbed a large percentage of the radiation of wave lengths below 2536 Å, some of the experiments were carried out in a set-up as illustrated in pl. 42, fig. 3, and referred to in the tables as position B. By means of a projection built on the microscope stage the objects were brought into a position directly in front of the exit slit of the monochromator. With this arrangement, however, it was impossible to make careful examination of the objects during the experiments.

Table I gives the intensities for the two positions A and B as illustrated in pl. 42, figs. 2 and 3. The total intensities of the light falling on the object at a slit width of 0.2 mm. or per 2 $mm.^2$ area are given for each spectral line.

Selection of Objects and Procedure

The selection of objects was limited, due to the necessity of having them exposed to a small area of light (2 $mm.^2$). Since ultra-violet radiation does not penetrate deeply into plant tissue and is known to be absorbed readily by single layers of cells, objects of single-cell thickness had to be selected. It was also im-

TABLE I

INTENSITIES OF LIGHT PER 2 SQ. MM. IN POSITIONS A AND B

Wave lengths	Intensities for position A (pl. 42, figs. 1–2)		Intensities for position B (pl. 42, fig. 3)	
Å	galv. defl. mm.	ergs/sec/2 mm.²	galv. defl. mm.	ergs/sec/2 mm.²
3663.27, 3662.87, 3654.83, 3650.15	24.5	196.0	36.0	280.0
3341.48	1.5	12.0	2.8	22.4
3131.84, 3131.56, 3125.60	10.5	84.0	26.8	214.4
3021.50	5.0	40.0	11.7	93.6
2967.28	2.7	21.6	5.1	40.8
2893.60	0.9	7.2	2.0	16.0
2803.50	2.0	16.0	4.3	34.4
2652.00	3.0	24.0	7.7	61.6
2536.00, 2534.80	2.0	16.0	11.2	89.6
2482.70	0.5	4.0	3.0	24.0
2378.30	0.3	2.4	1.0	8.0

portant that the objects should be transparent to visible light so that their cell contents could be examined under the microscope. Several objects were tried but few of them proved satisfactory for the purpose.

To determine their suitability various objects were placed at a distance of 10 cm. from the open water-cooled mercury vapor arc and their reaction to the radiation was observed. The cells of *Chlamydomonas* were found to be very sensitive to the action of the light from the arc. After exposure of 10 minutes their motion ceased, and in about 20 minutes a complete destruction of the cell contents was observed. Due to the motility and small size of the cells it was impossible to confine them within the narrow area (2 mm.²) of irradiation. Although the cells of the filaments of *Spirogyra* were markedly injured by the radiation of the arc after 30-minute exposures, it was difficult to obtain conclusive results, since even non-radiated cells showed a large variation in their response to plasmolyzing agents. *Cladophora* and *Pleurococcus* did not show any marked changes in their cell structure after exposures to the arc for ½ hour. Strips of the epidermis of *Rhoeo discolor* lost their purple pigment after an

exposure to the arc of about 1 hour, but due to their overlapping the vitality of the cells was difficult to judge.

The objects selected as most suitable were leaves of the gametophyte of a common local species of *Mnium* and stamen hairs of *Tradescantia reflexa* Raf. Single leaves of *Mnium* were carefully detached from the stem under the dissecting microscope. Six to nine leaves were then placed in a drop of tap water on a large glass cover-slip 43 × 50 mm. serving as a slide, and covered with a quartz cover-slip. This made it possible to observe the objects with a microscope from both sides. To prevent any pressure on the object, glass capillaries were interposed between the two cover-glasses. The object (i, pl. 42, fig. 2) after a microscopic examination was placed on a vertical adjustable microscope stage (h, pl. 42, figs. 2 and 3) provided with an opening in the center. Three of the leaves were then moved to such a position that the radiation, passing through the slit (2 mm.^{2}) of the monochromator, was focused on them. Thus an area of approximately 0.3 mm.^{2} of each leaf was exposed to the irradiation. The other leaves served as controls.

A similar procedure was adopted for the stamen hairs of *Tradescantia*. They were removed from the filament by means of a pair of pointed scissors, examined to detect possible injury, and then irradiated. At least three hairs were placed in such a position that they were in the path of the light. In each experiment at least eight cells were irradiated.

The exposure of the leaves of the moss plant to the full arc at a distance of 10 cm., for at least 4 hours, produced a decolorization of the chloroplasts. In extreme cases all the chloroplasts were completely deprived of the green color, but transitional stages could be observed. The cell walls appeared as if stained green by the diffused chlorophyll. In the case of one leaf overlapping another, the part shielded had green chloroplasts, although the effect of irradiation was indicated by the green color of the cell walls.

There was no visible change in the starch content of the chloroplast, but in the case of completely decolorized cells no plasmolysis could be produced, indicating destruction of the protoplasmic membrane. A similar effect was obtained by

exposing the leaves for 12 hours to a 1000-Watt Mazda lamp at a distance of 40 cm. However, to produce an effect comparable to that of the arc, an exposure of 12 hours was necessary. After the experiment the irradiated and control leaves were examined. Two of the irradiated leaves were plasmolyzed by an 8 per cent solution of KNO_3, and the third one was placed in a watch-glass with tap water for 3 to 8 hours to observe any possible after-effects of the irradiation. Cells of detached moss leaves used as controls did not show any detectable injury and responded readily to plasmolyzing if left in water for 24 hours.

The *Tradescantia* hairs had purple, vacuolar contents, so that the protoplasmic streaming was readily discernible. Unradiated hairs kept on the stage of the microscope for more than 24 hours showed no visible change in protoplasmic streaming, provided they were handled carefully and not subjected to pressure of the cover-glass. On exposure to the open mercury arc (at a distance of 10 cm.) the streaming ceased in 20 minutes and coagulation of the protoplasm was evident.

All the experiments with monochromatic light on the moss plant were carried out with the object and stage in position B, that is, directly in front of the exit slit of the monochromator (pl. 42, fig. 3). The experiments with the stamen hairs were carried out in position A (pl. 42, fig. 2) for the longer wave lengths and in position B (pl. 42, fig. 3) for the shorter wave lengths. As can be seen from table I, the intensities at position B were greater than at position A, and were therefore preferred for the moss leaf which was easily centered on the image of the slit by the low power of the microscope. In this position it was not possible to observe the behavior of the cells during irradiation, and the effect was determined by examining the exposed area at the close of the experiments. Position A was preferred for the experiments with stamen hairs, since by interposing a micro-lamp between monochromator and focusing lens (f and j, pl. 42, fig. 2) examinations with 16-mm., 8-mm., and 4-mm. objectives could be made. In the first experiment, with every spectral line tested, microscopic examinations were made at 10- to 15-minute intervals. In the succeeding ones, no examinations were made up to the close of the experiment. In this way a possible

effect of the micro-lamp was eliminated. The adjustment of the hairs over the slit in position B was somewhat difficult because the position of separate cells could not be accurately ascertained. The position of whole hairs, however, was easily determined.

It was of course impossible to test all of the lines of the mercury vapor spectrum or separate the closely adjacent ones. As can be seen from table I, eleven lines (or groups of lines) had been selected. All of them were easily separable with the slits at 0.2 mm. Two to three experiments were conducted for each of the lines used. The time of exposure was in most cases two hours, although in a few instances it was extended to as much as four hours. Longer exposures were not used due to technical limitations.

Experimental Results and Discussion

The results obtained are represented in tables II and III. No visible distortions in the cell structure were observed with any of the wave lengths or intensities used. All of the irradiated leaves of *Mnium* had a normal appearance. No distortions in the protoplast were visible, and the cells plasmolyzed readily if placed in an 8 per cent solution of KNO_3. No after-effects of the radiation were noticed. It might be possible that a slight discoloration of the chloroplast took place, but if so it was not clearly detectable. In one experiment after an intermittent exposure of eight hours (129.02×10^4 ergs/mm.^{2}) a discoloration comparable to that produced by the open mercury arc was produced. Since this is a single instance and the experiment has not been repeated, it is not taken into consideration in this paper.

In the case of the stamen hairs of *Tradescantia*, protoplasmic streaming was observed in all the cells irradiated. No visible distortion in the cell content was noticed. It seemed that in the case of line 2893 Å the protoplasmic streaming was retarded. The rate of streaming of the protoplasm, however, varied considerably in different cells, hence there is some difficulty in using it as a criterion of vitality.

There is no doubt that stronger intensities, at least for some ultra-violet lines, would produce a killing effect and destruction of the protoplast in plant cells.

From the data available for the energies of ultra-violet monochromatic light required to produce the killing of bacteria and

TABLE II

CORRELATION OF WAVE LENGTH, INTENSITY, TIME OF EXPOSURE, AND INCIDENT LIGHT ENERGY PER SQ. MM., USED IN THE EXPERIMENTS WITH LEAVES OF MNIUM

Wave lengths Å	Incident light intensity ergs/sec/mm.²	Experiment No.	Time of exposure hours	Total incident light energy ergs/mm.² × 10⁴
3654	140.0	I	2	100.80
		II	2	100.80
		III	2	100.80
3341	11.2	I	2	8.06
		II	2	8.06
		III	3	12.10
3131	107.2	I	2	77.18
		II	2	77.18
		III	2	77.18
3021	46.8	I	2	33.70
		II	2	33.70
2967	20.4	I	2	14.69
		II	2	14.69
2893	8.0	I	2	5.76
		II	2	5.76
		III	4	11.52
2803	17.2	I	2	12.38
		II	2	12.38
		III	2	12.38
2652	30.8	I	2	22.18
		II	2	22.18
2536	44.8	I	2	32.26
		II	2	32.26
		III	3	48.38
2482	12.0	I	2	8.64
		II	2	8.64
		III	2	8.64
2378	4.0	I	2	2.88
		II	2	2.88
		III	4	5.76

Constants: Total area irradiated = 2 mm.² Approximate area of each leaf exposed to irradiation = 0.3 mm.² Microscope stage and object in position B (pl. 42, fig. 3).
Effect: No visible changes in cell structure. Normal plasmolysis with 8 per cent KNO_3.

TABLE III

CORRELATION OF WAVE LENGTH, INTENSITY, TIME OF EXPOSURE, AND INCIDENT LIGHT ENERGY PER SQ. MM., USED IN THE EXPERIMENTS WITH STAMEN HAIRS OF TRADESCANTIA

Wave lengths Å	Incident light intensity ergs/sec/mm.²	Experiment No.	Time of exposure hours	Total incident light energy ergs/mm.² × 10⁴
3654	98.0	I*	2	70.56
		II*	2	70.56
		III*	1	35.28
3341	6.0	I*	2	4.32
		II*	2	4.32
3131	42.0	I*	2	30.24
		II*	2	30.24
		III*	2	30.24
3021	20.0	I*	2	14.40
		II*	2	14.40
		III*	2	14.40
2967	10.8	I*	2	7.78
		II*	2	7.78
2893	3.6	I*	1	1.18
	8.0	II	3	8.64
2803	8.0	I*	2	5.76
		II*	2	5.76
		III*	1	2.88
2652	12.0	I*	1	4.32
	30.8	II	2	22.18
2536	8.0	I*	2	5.76
	44.8	II	2	32.26
	44.8	III	3	48.38
2482	12.0	I	1	4.32
		II	2	8.64
2378	4.0	I	2	2.88
		II	3	4.32

Constants: Total area irradiated = 2 mm.² Approximate number of cells irradiated = 8.
Effect: No visible injury to the cell. Protoplasmic streaming continued.
In experiments indicated by asterisk (*) microscope and object were in position A (pl. 42, fig. 2); in the others, in position B (pl. 42, fig. 3).

paramecia (Gates, '29, Weinstein, '30), it was anticipated that the comparatively strong energies used in the present investigation would be sufficient to produce a similar effect on plant cells. This is apparently not the case.

TABLE IV

COMPARISON OF TOTAL ENERGIES (EXPOSURE TIME × INTENSITY) USED IN THIS INVESTIGATION WITH THOSE USED BY GATES AND WEINSTEIN

Wave length	Ergs/mm.²			
	Used in present investigation		Gates*	Weinstein
Å	*Tradescantia*	*Mnium*	necessary to kill 100% of bacteria	necessary to kill paramecia
3654	705,600	1,008,000		
3341	43,200	80,600		
3131	302,400	771,800		19,629
3021	144,000	337,000	13,000	10,850
2967	77,800	146,900	3,000	
2893	25,900	57,600	725	
2803	57,600	123,800	475	2,473
2652	86,400	221,800	350	2,162
2536	322,600	322,600	325	2,284
2482	86,400	86,400	350	
2378	28,800	28,800	540	

* Calculated from curves Gates ('29), p. 240.

TABLE V

COMPARISON OF INTENSITIES (ENERGY PER SECOND) USED IN THIS INVESTIGATION WITH THOSE USED BY GATES AND WEINSTEIN

Wave length	Ergs/mm.²/sec.			
	Intensities used in this investigation		Intensities used by Gates	Intensities used by Weinstein
Å	*Tradescantia*	*Mnium*	Bacteria	Paramecia
3654	98.0	140.0		
3341	6.0	11.0		
3131	42.0	107.2		7.27
3021	20.0	46.8		5.48
2967	10.8	20.4		
2893	8.0	8.0		
2803	8.0	17.2		1.33
2652	30.8	30.8	11.0	2.72
2536	44.8	44.8		1.12
2482	12.0	12.0		
2378	4.0	4.0		

If we compare the total energies (time of exposure × incident intensity) of this investigation with those used by the two

authors (table iv), it is apparent that much larger energies were used in this experiment.

Although the Roscoe-Bunsen photochemical reciprocity law has been shown to be fairly accurate for some biological objects, there still might be some doubt as to its applicability for exposures as long as two hours. Allowance in this case must be made for a possible concurrent recovery process of the organism during irradiation. However, table v shows that the intensities used in this experiment were larger by a factor of 3 to 40, and therefore the greater energies were due to increase both of intensity and time of exposure. It is therefore evident that the plant cells used are much more resistant to the lethal action of ultra-violet than bacteria and paramecia.

Several attempts have been made to explain the lethal action of ultra-violet radiation. Its killing action is usually ascribed to the destruction or precipitation of some of the constituents of the protoplasm. Henri ('12) found that the abiotic power of ultra-violet rays is proportional to the coefficient of absorption of the protoplasm. Gates ('28) believes that the destruction of certain nucleoproteins is responsible for the killing of the cell. However, it is clear that the resistance of a cell to the action of the rays will depend also on its structural characteristics, such as size of the cell, nature of its cell wall, presence or absence of pigments, etc. Henri ('12) showed that in small cells the entire protoplasm was affected by the rays, whereas in larger cells only a surface reaction resulted. Schulze ('09) noticed that the cell wall and especially the middle lamella are the parts of the cell which absorb most of the radiation if exposed to line 2800 Å. The comparatively high resistance of our objects to the lethal action of ultra-violet radiation might then probably be explained by the characteristic structure of the cells of higher plants.

Summary

1. The necessity of quantitative data for the study of the effect of ultra-violet light on plants is discussed.

2. An experimental arrangement for securing monochromatic light of measured intensities and its application for use with plant objects are described.

3. Leaves of *Mnium* and stamen hairs of *Tradescantia* are exposed to the radiation of eleven lines of the mercury spectrum.

4. It has been shown that no visible injury to the cells resulted from exposure to relatively strong intensities.

5. By comparing these results with those obtained by other workers it has been shown that the plant cells used are very much more resistant to the lethal action of ultra-violet light than bacteria and paramecia.

Acknowledgments

I wish to express my deep appreciation to Dr. E. S. Reynolds, under whose direction the investigation was carried out, for his assistance and suggestions during the progress of the work and preparation of this paper. I am also indebted to Dr. George T. Moore for the use of the facilities and library of the Missouri Botanical Garden, and to Dr. Lester C. Van Atta for assistance and suggestions in setting up the apparatus. The monochromator used in this investigation was loaned through the courtesy of the Bausch and Lomb Optical Company and the Committee on the Effects of Radiation upon Living Organisms of the Division of Biology and Agriculture, National Research Council. The Burdick water-cooled mercury arc was kindly placed at my disposal by the Dick X-Ray Company of St. Louis, Mo.

Bibliography

Arthur, J. M., and Newell, J. M. ('29). The killing of plant tissue and the inactivation of tobacco mosaic virus by ultra-violet radiation. Am. Jour. Bot. **16**: 338–354. 1929.

Barr, C. E., and Bovie, W. T. ('23). Ultra-violet cytolysis of protoplasm. Jour. Morph. **38**: 295–300. 1923.

Bovie, W. T. ('16). The action of Schumann rays on living organisms. Bot. Gaz. **61**: 1–29. 1916.

Coblentz, W. W., and Fulton, H. R. ('24). A radiometric investigation of the germicidal action of ultra-violet radiation. U. S. Dept. Com. Bur. Stand. Scientif. Pap. 495: 641–680. 1924.

Eltinge, E. ('28). The effects of ultra-violet radiation upon higher plants. Ann. Mo. Bot. Gard. **15**: 169–240. 1928.

Frank, G. ('29). Das mitogenetische Reizminimum und -maximum und die Wellenlänge mitogenetischer Strahlen. Biol. Zentralbl. **49**: 129–141. 1929.

————, und Gurwitsch, A. ('27). Zur Frage der Indentität mitogenetischer und ultravioletter Strahlen. Arch. f. mikroskop. Anat. u. Entw. **109**: 451–454. 1927.

Fuller, H. J. ('31). Stimulatory effect of radiation from a quartz mercury vapor arc upon higher plants. Ann. Mo. Bot. Gard. **18**: 17–40. 1931.

Gates, F. L. ('28). On nuclear derivatives and the lethal action of ultra-violet light. Science. N. S. **65**: 479–480. 1928.

————, ('29a). A study of the bactericidal action of ultra-violet light. I. The reaction to monochromatic radiation. Jour. Gen. Physiol. **13**: 228–246. 1929.

————, ('29b). *Ibid.* II. The effect of various environmental factors and conditions. *Ibid.* 249–260. 1929.

————, ('30). *Ibid.* III. The absorption of ultra-violet light by bacteria. *Ibid.* **14**: 32–42. 1930.

Henri, V. Mme. et M. ('12). Variation du pouvoir abiotique des rayons ultraviolets avec leur longueur d'onde. Compt. Rend. Acad. Paris. **155**: 315–318. 1912.

Hertel, E. ('05). Über physiologische Wirkung von Strahlen verschiedener Wellenlänge. Zeitschr. f. allgem. Physiol. **5**: 95–122. 1905.

Hill, L., and Eidenow, A. ('23). The biological action of light. The influence of temperature. Roy. Soc. London, Proc. B. **95**: 163–180. 1923.

Marshall, A. L., and Knudson, A. ('30). The formation of vitamine D by monochromatic light. Am. Chem. Soc. Jour. **52**: 2304–2314. 1930.

Reiter, J., and Garbor, D. ('28). Zellteilung und Strahlung. Sonderh. d. Wiss. Veröf. d. Siemens-Konzern. Berlin, 1928.

Ribaud, L. ('13). Étude quantitative de l'absorption de la lumiére par la vapeur de brome dans l'ultraviolet. Compt. Rend. Acad. Paris **157**: 1065–1068. 1913.

Schulze, J. ('09). Über die Einwirkung der Lichtstrahlen von 280 $\mu\mu$ Wellenlänge auf Pflanzenzellen. Beih. Bot. Zentralbl. **25**: 30–80. 1909.

Taylor, H. S. ('31). A treatise on physical chemistry. Second ed. New York, 1931.

Timirazev, C. ('75). On the assimilation of light by plants. [Russian]. St. Petersbourg, 1875.

Verhoeff, F. H., and Bell, L. ('16). The pathological effect of radiant energy upon the eye. Am. Acad. Arts and Sci. Proc. **51**: 629–810. 1916.

Ward, H. N. ('93). The action of light on bacteria. Roy. Soc. London, Proc. B **54**: 472–475. 1893.

Weinstein, I. ('30). Quantitative biological effect of monochromatic ultra-violet light. Opt. Soc. Am. Jour. **20**: 433–456. 1930.

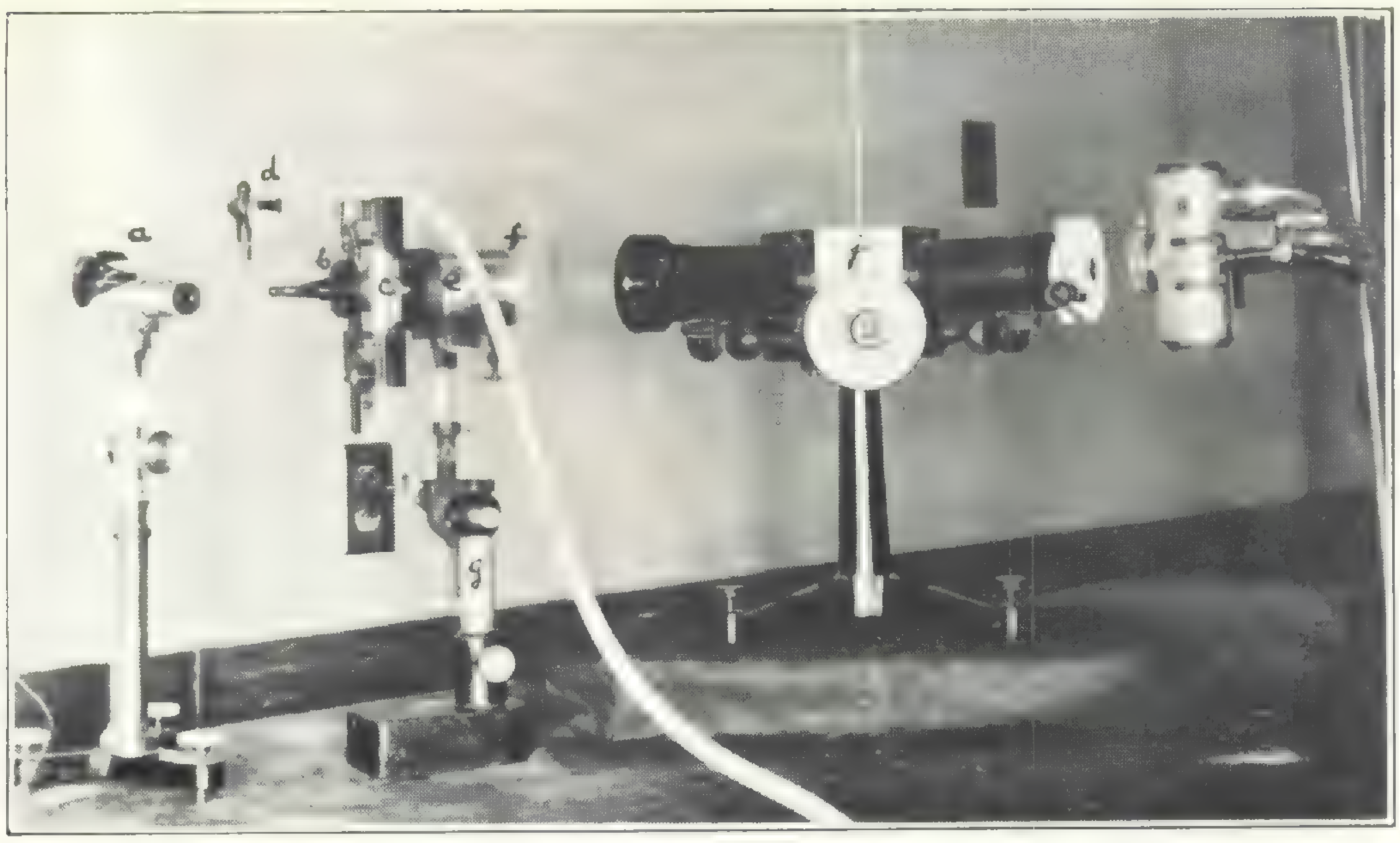
Explanation of Plate

PLATE 42

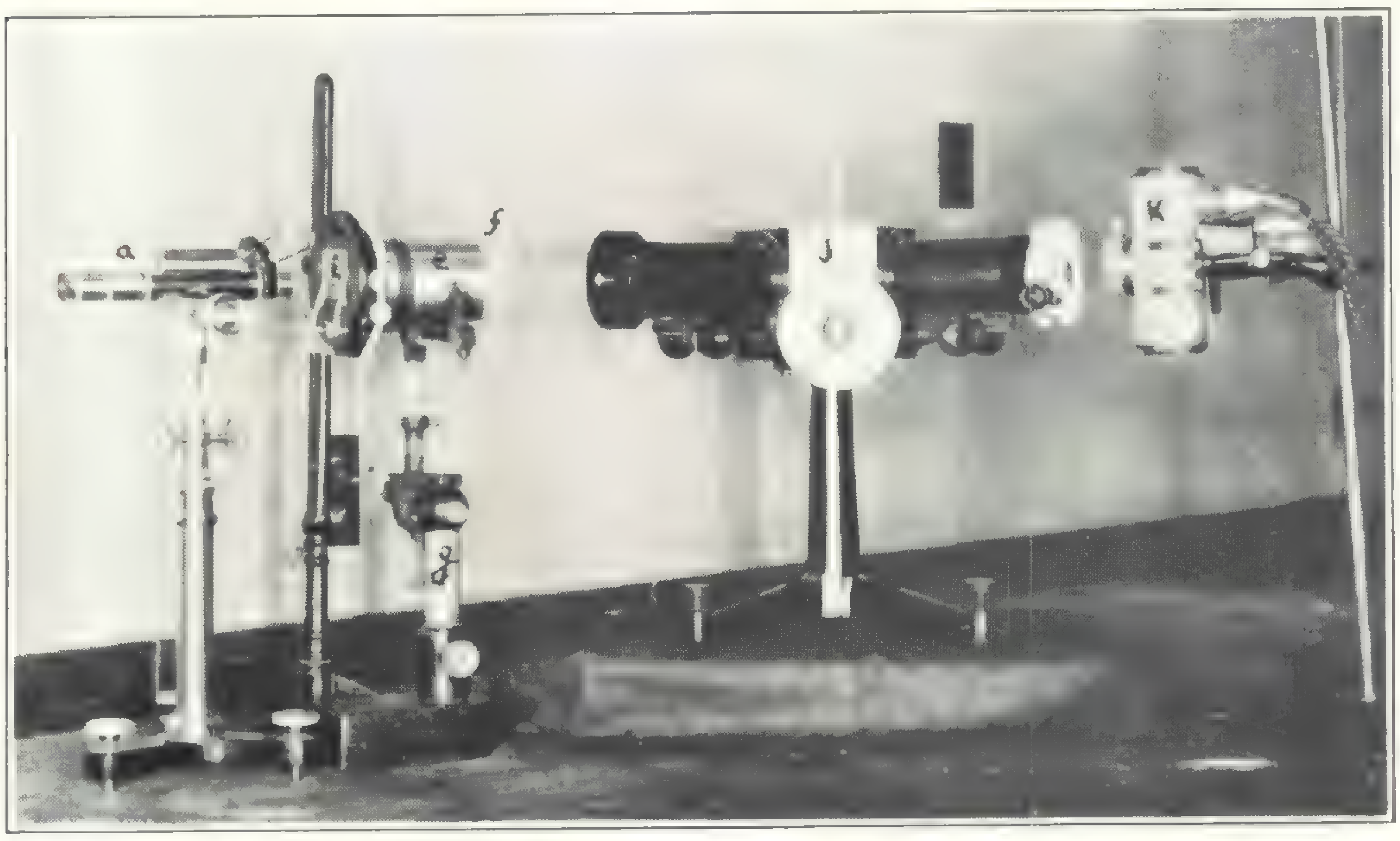
Fig. 1. Position of monochromator, focusing device, and thermopile during intensity measurement (A).

Fig. 2. Position of monochromator, focusing device, and stage supporting object during irradiation (A).

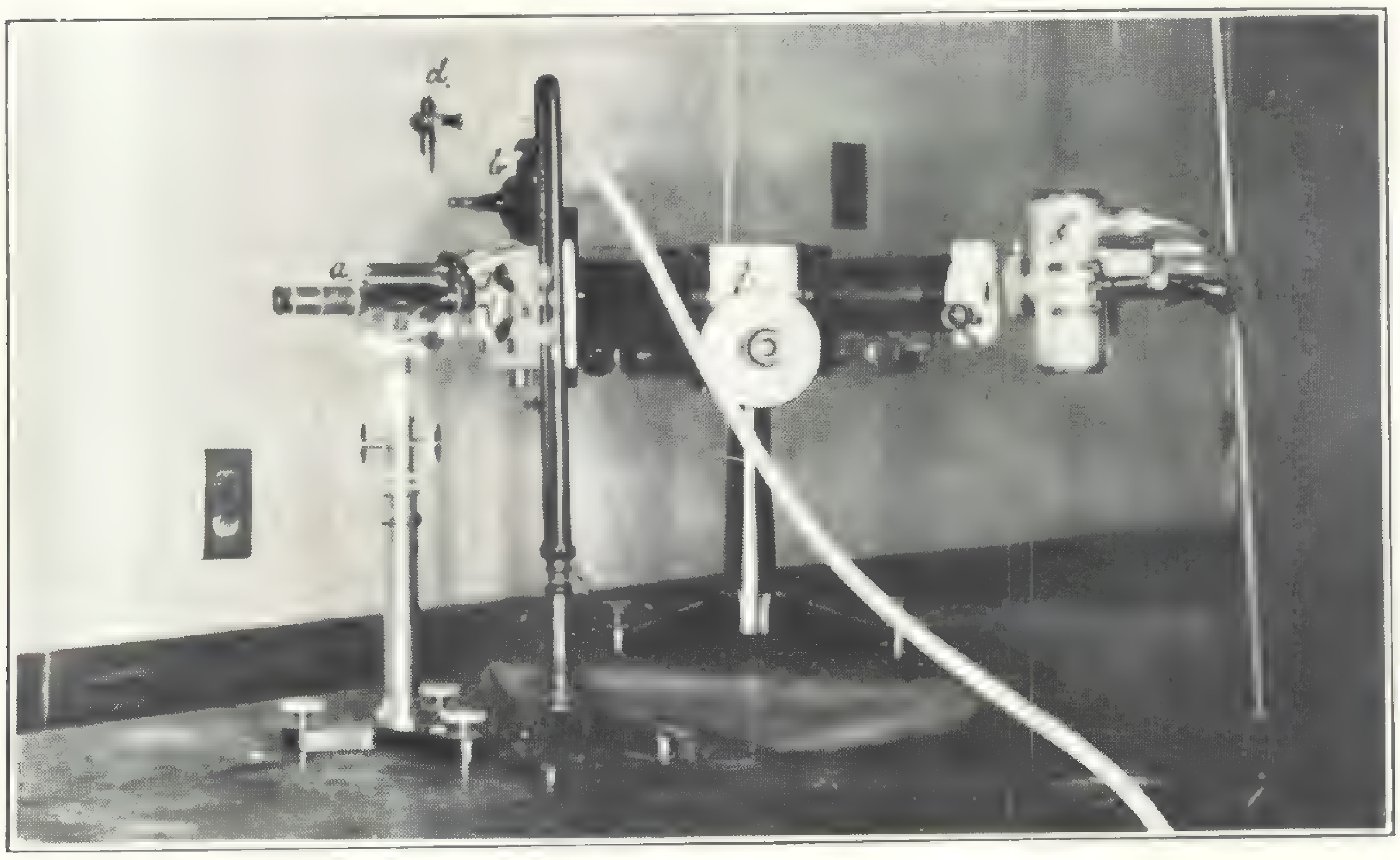
Fig. 3. Microscopic stage and object in position B close to exit slide of monochromator.



1



2



3

BUCHOLTZ—MONOCHROMATIC ULTRA-VIOLET LIGHT

THE CYTOLOGY OF FUNARIA FLAVICANS MICHX. WITH SPECIAL REFERENCE TO FERTILIZATION[1]

MARTHA LYDIA BEARDSLEY

Professor of Biology, Sioux Falls College, Sioux Falls, South Dakota
Formerly Instructor in Botany, Henry Shaw School of Botany of Washington University

I. Introduction and History

The desirability of a study of fertilization in the Mosses was suggested by the fact that this is the one great group of plants in which no thorough investigation had been undertaken concerning nuclear fusion. The question of fertilization in the Liverworts, which are similar to the Mosses in their structural aspects, has received considerable attention in recent years. In the Liverworts three distinct types of nuclear fusion are encountered. Inasmuch as the observations regarding fertilization in the Mosses are so meagre and since the processes in the Liverworts are so diverse, the present investigation was undertaken.

The literature contains fragmentary observations on the subject, the earliest of which is that of Hofmeister ('62), who observed in *Funaria* an antherozoid moving down the neck of an archegonium which was ready for insemination. In the case of dioecious species no fruit or sporophyte was formed unless male and female plants were growing in the same locality. He observed that the young sporophyte when consisting of from one to four cells remained free in the ventral cavity, but, after further division, grew down into the tissue of the archegonium.

Roze ('72), studying the development of the archegonium in *Sphagnum*, depicted an archegonium with several antherozoids in the neck canal and one antherozoid in contact with the egg. The antherozoids entered with the ciliated portion foremost and remained in the ventral cavity. The thickness of the archegonial wall prevented him from determining the progress of penetration of the antherozoid into the egg.

[1] An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

Arnell ('75) observed, during an examination of archegonial material of *Discelium nudum* (Dicks.) Brid., one plant of which the archegonium had a visible canal. During his observations the top cells separated and the archegonium opened. The antherozoids were drawn to the mouth of the archegonium as if attracted by a magnetic power. In addition he noticed a rocking motion of the egg due to the movement of the antherozoids which were surrounding it.

Gayet ('96), in connection with his study of archegonial development in *Bryum capillare* L., observed antherozoids swimming down the neck canal and one of them penetrating the egg. After penetration the antherozoid assumed a crescent shape and became located above the egg nucleus.

In *Fissidens incurvus* Schwaegr., Gayet perceived that in fertilization a large number of antherozoids penetrated the egg, but that only one united with the egg nucleus. The antherozoid, in the cytoplasm of the egg, became crescent-shaped at first and then spherical. The female nucleus possessed four chromosomes which were attracted to the male nucleus. After fusion only four chromosomes were discernible in the fertilized egg, and Gayet inferred that each male chromosome fused with a female.

W. and J. Van Leeuwen-Reijnvaan ('08a) reported a very bizarre process in the fertilization of *Polytrichum*. From their observations they inferred that reduction divisions occurred both in the archegonium and in the antheridium. The ventral canal cell and the egg then fused, and the product of this fusion was fertilized by two antherozoids. In this way the sporophyte had double the original number of chromosomes. The same authors reported a similar situation in *Mnium*.

Wilson ('09) found in *Mnium*, however, that reduction division took place in the division of the spore-mother-cells to form spores. In studying spermatogenesis in other Bryophytes he found no evidence of a reduction division in the formation of the antherozoids.

Vandendries ('12) studied spermatogenesis in *Polytrichum* with reference to the chromosome number. He showed quite conclusively that there was no double reduction occurring in the formation of the antherozoids.

Walker ('13) found no fusion of the egg with the large ventral canal cell of *Polytrichum*. He contended that the bizarre process described by J. and W. Van Leeuwen-Reijnvaan was doubtful since his studies showed no such process occurring.

Bryan ('20) described in complete detail the fusion of the ventral canal cell and the egg of *Sphagnum subsecundum* (Nees) Limpr. His results indicated that the number of cases in which this abnormal fusion occurred about equalled those in which the ventral canal cell had disintegrated. He reported two cases in which the egg nucleus disintegrated and in which the nucleus of the ventral canal cell remained distinct and sharply defined.

Harvey-Gibson and Miller-Brown ('27) published a preliminary note on the fertilization of Bryophytes. Their work consisted of observations made on mites which visited both male and female heads of *Polytrichum commune* L. The mites carried sperms on their bodies from antheridial heads to archegonial heads and in this way brought about insemination of distant archegonial heads.

The Liverworts, on the other hand, have received considerable attention within recent years. Rickett ('23) has summarized the earlier literature on the subject, and it need not be repeated here.

In *Sphaerocarpos*, according to Rickett, the male nucleus after penetration into the cytoplasm of the egg swells markedly, becoming spherical and reticulate but remaining smaller than the female nucleus. The two gametic nuclei come into contact but remain distinct until each has organized its chromosomes preparatory to mitosis. The two nuclear membranes then disappear and a spindle figure is formed, thus initiating the metaphase of the first embryonic division.

Showalter ('26, 27a, 27b, '28) has made careful studies of the fertilization processes in three of the Anacrogynae. In *Riccardia* ('26) the male nucleus remains, with scarcely any perceptible change of form, in the cytoplasm of the egg for from twenty-nine to thirty-six hours. Then it penetrates endwise and passes slowly into the female nucleus, where it forms first a vesicle of deeply staining chromatic material, and later a compact reticulum that loosens up more and more until after three to four days it

is no longer distinguishable from the reticulum of maternal chromatin.

In *Pellia* ('27b) the male nucleus, after penetration into the egg, moves slowly toward the female nucleus and gradually assumes a reticulate form. The cytoplasm between these two nuclei recedes, leaving the mass of paternal chromatin almost in contact with the membrane of the female nucleus. The membrane of the female nucleus seems to dissolve in the region of contact with the paternal chromatin, and a common membrane encloses the paternal chromatin and the female nucleus. The union of the two nuclei occurs usually the second day after insemination. The paternal chromatin quickly assumes the condition of the maternal chromatin, and except for the presence of two nucleoli the dual nature of the fusion nucleus is distinctly evident for a short time only.

In *Fossombronia* ('27a) actual penetration of the male nucleus into the female nucleus was not observed, although Showalter found that after forty-eight hours the chromatic mass about the nucleolus had become a reticulum which occupied approximately one hemisphere of the nuclear cavity. In the other hemisphere was a dense mass of chromatic substance which was more intensely stained than the chromatic reticulum, and it seemed probable that this dense mass was the substance of the male nucleus.

Showalter ('28) has studied hybrid fertilization in four varieties of *Riccardia pinguis* (L.) S. F. Gray. In this study he found that nuclear fusion between the four types was in accord with that described in his earlier paper on *Riccardia* ('26).

The salient points in these investigations are shown in table II, where they are compared with the results obtained in *Funaria*.

II. Materials and Methods

Funaria flavicans Michx. is similar in its morphological features to *Funaria hygrometrica* (L.) Sibth., with which it is often associated in nature. It may be distinguished from *Funaria hygrometrica* by its smaller size, its erect pedicel, and its more pointed leaves. The capsule, which is furrowed less deeply than that of *Funaria hygrometrica* and which has a non-apiculate lid,

matures a week or two earlier. *Funaria hygrometrica* is almost cosmopolitan in its distribution, whereas *Funaria flavicans* has been reported only from the mid-central and southern portions of the United States. Both species are monoecious. *Funaria flavicans* is abundant around St. Louis, Missouri, and was found to grow well in cultures. Hence, it was selected for the experimental work described in this thesis.

Mature sporophytes were obtained in the spring of 1929, near Festus, Missouri, where a great number of plants were growing on an outcrop of St. Peter sandstone. Specimens of the material were sent to Dr. A. J. Grout, who kindly verified the identification. The spores were sown on a sterile mixture of sand and soil in six-inch pots which were then set in granite pans containing tap-water. This procedure permitted the soil to remain moist and at the same time prevented spontaneous insemination. The cultures were kept in a north greenhouse in which the temperature was relatively cool. When both archegonia and antheridia were mature insemination was brought about by flooding the cultures. The pots were tightly corked from below, placed in a container of water, and then covered with water. These precautions were taken in order that the water would not seep down into the soil, carrying the antherozoids with it. At the end of half an hour, that being the time determined necessary for the antherozoid to escape from the gelatinous envelope surrounding it, the pots were removed from the container, uncorked, and the excess water permitted to drain out at the bottom of the pots. Fixations were made at intervals after flooding. The killing fluids employed were chromo-acetic, Flemming's medium, Showalter's modification of Flemming's medium ('26), Navaschin's chromo-acetic formalin as described by Babcock and Clausen ('29), and Benda's fluid. Although Flemming's medium and Benda's fluid produced perceptible plasmolysis, Showalter's modification and Navaschin's fixative gave excellent results.

After washing, dehydration, infiltration and imbedding in paraffin, the material was sectioned and stained. Sections cut 12 μ in thickness often included the entire egg in one section. The material was stained, some with Flemming's triple stain,

some with Haidenhain's iron-alum haematoxylin, and some with the gentian violet-iodine combination. The iron-alum haematoxylin did not give as clear nuclear differentiation as was obtained with the triple or with the gentian violet-iodine combination.

In studying the slides, recourse was made to the standardized scheme of systematic and objective observation developed by Fry ('30) in connection with his studies of fertilized echinoderm eggs and recently outlined by him.

III. Observations

1. Spore Germination and Development of the Leafy Shoot

The first visible indication of germination of spores sown on soil is the modification in spore color. The spores when sown have a definite orange color, but with the development of more chlorophyll in the protoplasts the orange color is gradually transformed first to a brown, then to a deeper brown, until the distinction between the brown color of the spore and the green color of the developing protonemata is scarcely perceptible. These faint patches of green color are discernible three days after the spores are sown. The development of the protonemata continues rather rapidly, and under favorable temperature conditions, around 20° C., the entire pot is covered with protonemata within four weeks. After six to seven weeks the first leaves of the gametophores appear. Their development continues, and within three months the antheridia are discernible at the tips of leafy branches as small green knob-like structures. As the antheridia mature they change in color from green to bright orange, and with the discharge of the antherozoids they become very dark brown.

Since *Funaria flavicans* Michx. is monoecious the archegonia are developed on the same plant as are the antheridia. However, the archegonial heads arise as lateral branches of the male gametophore. Their development takes place at a later date, and the relationship of the archegonial branch to the antheridial when the antheridia are maturing is indicated in fig. 1. Following insemination and fertilization the archegonial branch develops rapidly and quickly surpasses the antheridial branch in size, until the latter is quite insignificant in comparison with the former.

The young sporophyte is visible to the unaided eye within ten days after fertilization. At this time its structure is exceedingly long and narrow, indicating a very small mass of potential sporogenous tissue, but this tissue increases in amount with

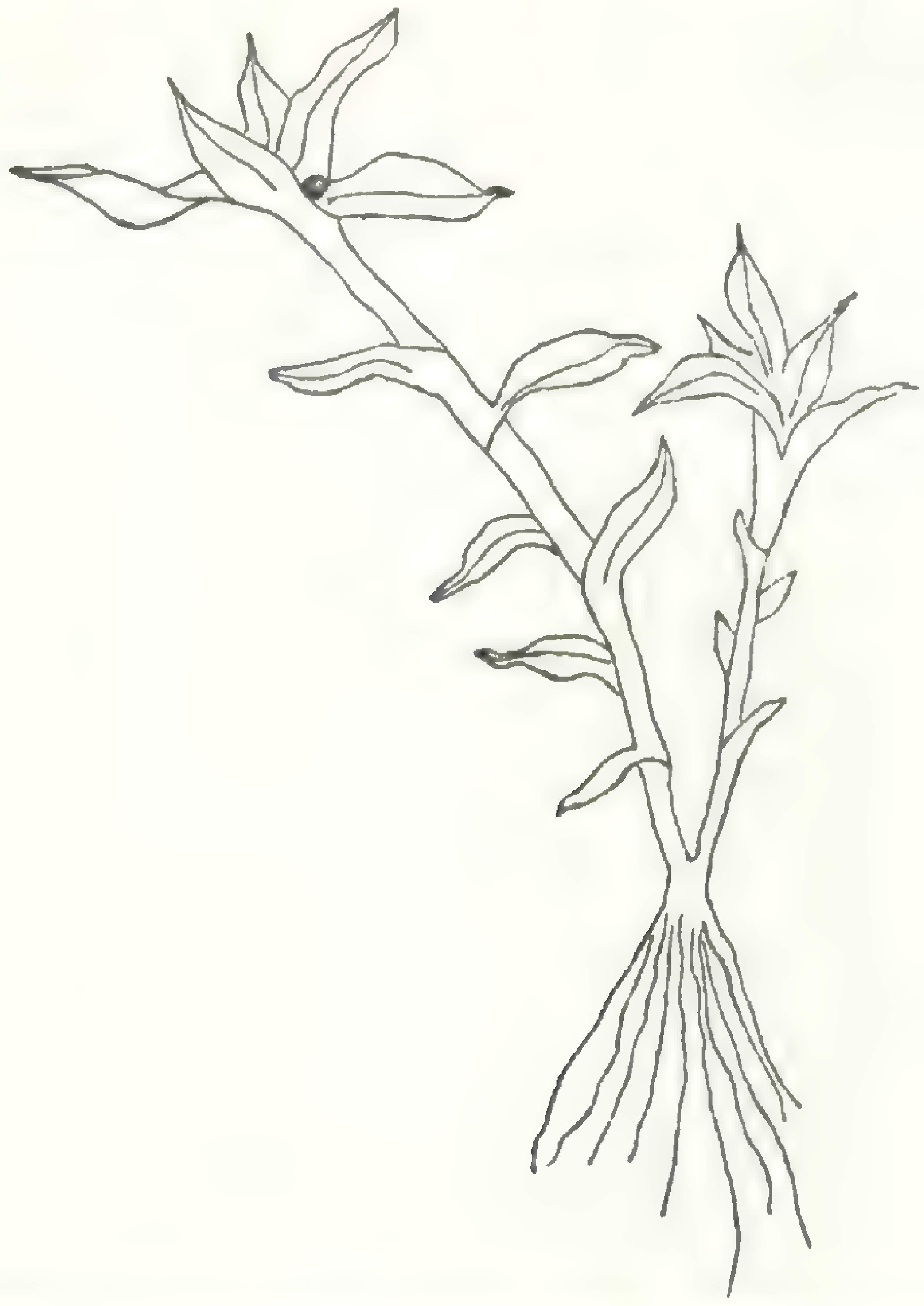


Fig. 1. Relationship of archegonial branch (right) to the antheridial branch when antheridia are maturing.

continued growth of the sporophyte. The sporophyte with fully developed spores reaches maturity five weeks after insemination.

2. DEVELOPMENT OF THE ANTHERIDIUM

The antheridium develops from a superficial cell (pl. 43, fig. 1). Nuclear division takes place and a cross wall is laid down between the two daughter nuclei (pl. 43, fig. 2). The division of these cells continues, with walls being laid down at various angles, until a many-celled structure is developed (pl. 43, fig. 3). The outer layer of cells develops into the wall of the antheridium, and the two cells at the apex are characterized by their unusual size (pl. 43, fig. 4). These two cells function in the discharge of

the antherozoids. The antherozoid when discharged is surrounded by a gelatinous envelope which is readily dissolved, after which the antherozoid may be observed swimming about (pl. 43, figs. 5–6). In material which has been fixed and stained the two cilia are very distinct, but in living material these structures are not readily observed.

In the antheridial head are found sterile hairs or paraphyses which are multicellular and contain numerous chloroplasts. In very young heads it is observed that these paraphyses are filiform and very similar to those found in the archegonial heads (pl. 43, fig. 7). The changes undergone in the transition from the filiform to the clavate condition are unusually interesting and apparently have never been described (pl. 43, figs. 8–9). The nucleus in the one-celled filament possesses a very large nucleolus which in a later stage is apparently in the process of division and represents what might be interpreted as an intra-nuclear division (pl. 43, fig. 10), such as is found in certain of the lower fungi. The cytoplasm of the young paraphysis contains very definite rod-shaped structures that increase in thickness and later are distinguished as early stages in plastid development. In comparing living material with fixed material the stages in plastid development are readily observed. In the unicellular paraphysis the chloroplasts are elongated structures which appear as rods in fixed material. These chloroplasts change from the elongated rods into small spherical bodies. In the mature clavate paraphysis the chloroplasts have increased in size and their structure is characteristic of the mature plastid.

There is a considerable number of mature antheridia in one head with the majority in the same stage of development, that is, nearly all the antheridia develop concurrently and mature almost simultaneously. Occasionally an antheridial head is found in which a number of developmental stages was found, but this was somewhat rare.

3. DEVELOPMENT OF THE ARCHEGONIUM

The archegonium, like the antheridium, develops from a superficial cell, and in the very early stages it is impossible to distinguish a young archegonium from a young antheridium

(pl. 43, fig. 11). In somewhat later stages the paraphyses may be used as a criterion, since they are characteristically different in the two kinds of heads. In the archegonial head they are always unicellular and filiform and may be distinguished from the young filiform paraphyses of the antheridial head by the less dense cytoplasm and by the fact that they are long and slender, whereas those of the antheridial head are shorter and more nearly uniform in transverse diameter (pl. 43, fig. 14).

The cell which gives rise to the egg and the ventral canal cell is located in the basal portion of the archegonium and completely fills the ventral cavity (pl. 43, fig. 15). The division of this cell is somewhat unequal, the egg receiving approximately three-fourths of the cytoplasm of the original cell, the ventral canal cell the remaining fourth. The fact that there is an invagination of cytoplasmic material at the point where the two cells divide gives one the impression that division is brought about by furrowing rather than by formation of a cell plate, but this invagination may be due to the rounding up of the newly formed cells (pl. 43, fig. 16). An insufficient number of observations prevents the writer from making any precise deductions.

The ventral canal cell, after formation, has a clearly defined nucleus. This disintegrates eventually and in later stages is recognized merely as a dense mass within the cytoplasm (pl. 44, fig. 17). When this nucleus ceases to be recognizable as such the beginning of disorganization of the neck canal cells may be observed, the ventral canal cell disintegrates along with the other canal cells, and the egg is ready for fertilization.

The number of archegonia in a head varies from one to many. These are generally at various stages of development, although there may be two mature archegonia in one head at the same time. Both of these archegonia may contain eggs in the same stage of fertilization. This is encountered in about 17 per cent of the material examined, and in one plant three mature archegonia were found with their eggs in precisely the same stage of fertilization. The archegonia apparently exercise no ill effects on each other, for several instances were noted in which two young sporophytes in a multicellular condition were found in the same head. These sporophytes showed no indication of being in a dwarfed condition.

4. FERTILIZATION AND NUCLEAR FUSION

In material fixed immediately after flooding, the spherical egg with densely granular cytoplasm is found either in the central portion of the ventral cavity or toward the bottom. The unfertilized eggs range in diameter from 7.0 to 8.6 μ, whereas the ventral cavities range from 8.0 to 12.6 μ. The nucleus, which occupies the central portion of the egg, is from 2.7 to 3.3 μ in diameter and possesses a very large nucleolus. Very little chromatin material, other than the nucleolus, could be definitely recognized. However, a distinct granular zone was differentiated about the nucleolus (pl. 43, fig. 18). At this particular stage only one archegonium was found in which the antherozoids had passed down the canal and were near the egg. The gelatinous envelope which surrounds the antherozoid when discharged from the antheridium requires from twenty to thirty minutes for dissolution. Inasmuch as this period of time is required and since the neck canal is exceedingly long, it is probable that in material fixed immediately after flooding the antherozoids have not had the opportunity to reach the egg in the archegonium.

With complete dissolution of the gelatinous envelope the antherozoids swim down the neck canal and into the venter. A large number of them approach the egg so that it has the appearance of being covered with very fine threads (pl. 43, fig. 19). Immediately following the entrance of the antherozoids into the venter a mucilaginous plug appears in the canal (pl. 43, fig. 20). This plug seems to be a secretion of the first two tiers of cells above the venter, inasmuch as it is always found associated with these two tiers of cells and never with any others. The plug, furthermore, is connected in some way with the process of fertilization. In all archegonia in which antherozoids have entered, the plug is present and remains not only throughout the fertilization process but also in early stages of sporophytic development. A few archegonia are found in which the ventral canal cell has not completely disintegrated and into the venter of which antherozoids have entered. In these no indication of the mucilaginous plug is discernible. The plug, which stains less deeply than the egg or any of its components, appears to have the ability to prevent the entrance of any more antherozoids, because

in the majority of cases there is present above the plug a large number of antherozoids tangled together. In some instances one to several antherozoids have been caught in this mucilaginous secretion.

The antherozoids approach the egg from all angles and tend to become closely adpressed to its surface which is slightly indented along the lines of contact (pl. 44, figs. 21–22). Those antherozoids, which become adherent to the egg, take a deeper stain than do those which are present in the ventral cavity and in the canal, since whenever the triple stain has been used the former are violet in color whereas the latter are red—depending upon the intensity of the stain. Notwithstanding the fact that the antherozoids lose their cilia on becoming adpressed to the egg, those present both in the canal and in the cavity are still equipped with cilia.

The antherozoid is a long slender structure with the anterior region somewhat enlarged and spherical. The two cilia which are present are attached to the antherozoid at this anterior region.

The antherozoid after becoming attached to the surface of the egg begins to pierce the membrane in its spherical portion (pl. 44, fig. 23). The substance of the antherozoid gradually passes into the cytoplasm of the egg, after which the original form is resumed. The antherozoid, in 63 per cent of the cases observed, penetrates the surface of the egg in the side toward the base of the archegonium. If penetration has not occurred in this region it takes place at one side (30 per cent of all cases observed) of the nucleus and only rarely above (7 per cent) the level of the nucleus. The time required for penetration is rather short, material fixed two hours and twenty minutes after insemination showing antherozoids in the cytoplasm of all the eggs in condition to be fertilized.

The entrance of an antherozoid into the cytoplasm of the egg seems to stimulate it to increase gradually in size. With this gradual increase in size there is a concurrent increase in the size of the ventral cavity as well as in the width of the archegonium. The size of the egg nucleus, however, is affected only slightly by this penetration of the antherozoid. Table I gives the average

measurements of these structures and indicates the gradual increases in size.

TABLE I

AVERAGE MEASUREMENTS

Fixation number	Interval after flooding	Egg diameter in microns	Ventral cavity diameter in microns	Archegonium diameter in microns
1	5 minutes	7.7	10.1	——
2	35 minutes	7.1	10.9	——
3	1 hr. 35 min.	8.5	12.3	——
4	2 hr. 20 min.	8.3	12.3	37.9
5	3 hr. 30 min.	8.5	12.8	35.6
6	4 hr. 30 min.	8.7	13.8	40.1
7	5 hr. 30 min.	8.8	13.8	40.3
8	6 hr. 30 min.	8.6	13.0	37.0
9	7 hr. 30 min.	9.3	12.6	40.0
10	8 hr. 30 min.	8.3	14.0	33.8
11	9 hr. 30 min.	8.9	12.6	38.6
12	10 hr. 30 min.	9.0	12.5	36.4
13	11 hr. 30 min.	8.9	13.9	39.2
14	14 hr.	9.1	12.3	42.6
15	16 hr.	8.8	14.1	39.9
16	18 hr.	8.9	13.1	44.7
17	18 hr. 30 min.	9.2	15.3	39.2
18	22 hr. 20 min.	9.5	13.0	41.3
19	23 hr. 30 min.	9.6	14.0	40.9
20	28 hr. 10 min.	9.3	13.7	38.1
21	45 hr. 20 min.	9.9	14.2	46.6
22	45 hr. 55 min.	9.9	15.5	45.9
23	48 hr. 45 min.	10.0	16.6	46.3
24	93 hr.	10.2	16.8	47.1

The variations in the widths of the ventral cavity and of the archegonium are explained by the fact that the region containing the egg is not always the median portion of the archegonium. If the egg is situated toward the outer area of the ventral cavity the archegonium will be narrower in width at this point than in the region directly at the center of the ventral cavity.

Penetration, moreover, is not restricted to a single antherozoid. Instances of polyspermy, however, are relatively few, only a small number being noted and these in the very early stages soon after

insemination. It is quite likely that the supernumerary antherozoids disintegrate, inasmuch as no case was found at a later stage in which they were present in the cytoplasm of the egg. Plate 44, fig. 26, shows an egg in which the spherical portions of several antherozoids have penetrated, the elongated portions not being readily distinguishable in the dense cytoplasm.

In two instances where the ventral canal cell had not completely disintegrated both the aforementioned cell and the egg were surrounded by antherozoids. There is no indication, however, that the antherozoids ever penetrate the ventral canal cell.

The antherozoid does not remain in the cytoplasm in a quiescent condition. It becomes shorter and thicker and passes to a position near the female nucleus immediately after penetration is completed (pl. 44, fig. 27). In material fixed three hours and thirty minutes after insemination the male nucleus has come in contact with the egg nucleus (pl. 44, fig. 28).

There was but one case observed in which the supernumerary antherozoids were still surrounding the fertilized egg. Those which do not penetrate the membrane apparently disintegrate, for with this one exception no instances have been found in which the supernumerary antherozoids remain adjacent to the egg longer than three hours and thirty minutes after insemination. On the other hand, those antherozoids which are present in the cavity are still recognizable as such in material fixed ten hours and thirty minutes after insemination.

The cytoplasm becomes less dense with the entrance of the antherozoid, and material fixed in Flemming's medium and stained with the iron-alum haematoxylin shows the presence of very definite rod-like and spherical bodies (pl. 44, fig. 35). The dense mass about the nucleolus becomes less granular and moves toward the periphery of the nuclear cavity, leaving a clear zone about the latter structure. The cells of the archegonium become vacuolated, and in the basal portions mitotic figures occasionally are found.

The male nucleus as it comes in contact with the female nucleus causes a depression in the surface of the latter. The antherozoid or sperm nucleus becomes shorter and thicker and is distinguished at one side of the female nucleus or below it as

a slightly elongated ovoid structure (pl. 44, figs. 29, 30). The male nucleus penetrates the female nucleus, and its chromatin substance passes into the female nuclear cavity where it assumes a more or less definitely ovoid form (pl. 44, figs. 31, 33, 34). The exact method of penetration could not be determined because of the minute size of the nucleus. Whether the membrane disappears at the point of contact has not been definitely determined. The membrane is not visible at the point where the male nucleus is in contact and later enters, but immediately after complete entrance a membrane is again very distinct and definite.

The male nucleus, moreover, does not remain in a resting state. The nucleolus of the egg nucleus, which is in reality the condensed reticulum enclosing the true nucleolus, tends to become vacuolate after entrance of the male nucleus into the female nucleus, and the mass of paternal chromatin is attracted to it (pl. 44, fig. 32). The dense mass which previously surrounded the condensed reticulum has practically disappeared, and about the two masses present in the nuclear cavity there is distinguished a zone which is quite clear. During the entrance of the paternal chromatin a definite staining area is evidenced, indicating the penetrating substance. The two distinct masses of chromatin tend to come together in the center of the cavity. The nuclear membrane becomes irregular in outline and eventually disappears completely (pl. 44, figs. 36–39). The two chromatin masses come into contact and gradually fuse, the two bodies being vaguely distinct and discernible only as darker-staining regions (pl. 44, fig. 40; pl. 45, fig. 41). The complete intermingling of the two masses of chromatin is more or less gradual.

The fused mass of chromatin is easily recognized by the fact that it is a somewhat spherical body with specific regions that are much darker than others. It remains in the central portion of the egg and without any perceptible membrane for several hours after fusion. During this time there is no apparent change in the structure of the fusion product. The cytoplasm is less granular at this stage and tends to become somewhat vacuolated toward the periphery of the egg. After ten to twelve hours the granular portion of the cytoplasm tends to become aggregated about this fusion nucleus. The aggregated cytoplasm

shows a tendency to become dense and gives the appearance of a definite granular zone similar to the one observed in the earlier stages. As this zone increases in density the outlines of a membrane being laid down become visible, at first considerably irregular, but gradually more regular and definite (pl. 45, figs. 44–48).

The fusion nucleus, as it is now recognized, remains in a resting stage for some time. A fertilized egg in this stage is distinguished from an egg just prior to insemination by its larger size, as well as by the appearance of the condensed reticulum.

In some of the material fixed forty-five hours and twenty-five minutes after insemination, the mucilaginous plug indicating that insemination has occurred, very definite plastid-like bodies are observed in the egg. These bodies are much too large and regular in appearance to be considered as chondriosomes. The condition of the nucleus is somewhat masked from view by the presence of these plastid-like bodies. In later stages, however, no such bodies are discernible, and it is a matter of speculation whether their preservation in this case is attributable to the particular fixative used, Benda's fluid, or whether the egg was not fertilized, as a result of which the plastid-like bodies developed.

The nucleus remains in the resting condition for a considerable period, after which it undergoes the changes for the prophase of the first division. The condensed reticulum, or the body which represents the fusion of the maternal and paternal chromatin, presents an appearance similar to that found in other nuclei at an early prophase stage in the division process. The chromatin becomes transformed into a spireme which is located not in the peripheral portion of the nuclear cavity as is customary, but within the region previously occupied by the condensed chromatin (pl. 45, fig. 50).

The first division of the nucleus and cell is transverse to the long axis of the egg and the archegonium. The two daughter nuclei which are formed tend to pass through a short resting stage before going through the second division which is at right angles to the first. There is an enormous increase in the size of the cell with the formation of the daughter nuclei. An embryo

in the bi-nucleate condition has a diameter of 25 μ, whereas the fertilized egg in the later stages before division has a diameter of 11 μ. The nuclei are quite large, possessing large nucleoli, and present an appearance similar to that found in the resting nuclei of the mature egg (pl. 45, figs. 51, 52). Further divisions occur rapidly until a multicellular sporophyte is formed. This sporophyte remains free in the ventral cavity and does not grow downward into the tissue of the archegonium until some time later. The archegonium increases considerably in size, and this increase is correlated with the increase in size of the young sporophyte.

5. SPORE FORMATION

The sporogenous tissue originates as a single row of cells toward the outer periphery of the columella. The cells are at first rectangular and are in an active stage of division. They increase in size and become rounded off so that at the time they are matured into spore-mother-cells they are quite spherical in shape.

The nucleus of the spore-mother-cell divides, and the resulting daughter nuclei go to opposite ends of the cell. These daughter nuclei do not appear to undergo a resting stage but pass from a very late telophase into the early prophase of the second division. In the second division the plane of division of one daughter nucleus is at right angles to that of the other daughter nucleus. This conclusion is reached from the fact that the majority of spore-mother-cells shows only three nuclei in focus, the fourth nucleus being seen when the focus is changed (pl. 45, figs. 54–56).

Cytokinesis of the spore-mother-cells is by cell-plate formation, the cytoplasm displaying no indication of furrowing either after the first division or after the second division. No walls are laid down after the first division, but those formed after the homeotypic division are laid down before the daughter nuclei are completely reconstructed.

6. CHROMOSOMES

An attempt was made to determine not only the structure of the chromosomes but also the specific number. Mitotic figures are frequently found in various tissues of the plant. The lower

portion of the archegonium shows a large number of mitotic figures, one of which gives an excellent polar view (pl. 45, fig. 57). By careful focusing, ten chromosomes can be brought into view. It is very likely that these represent both poles, inasmuch as the sections were cut rather thick. With the highest magnification available, it has been impossible to determine the exact number of chromosomes. Mitotic figures in the antheridium are less helpful than those of the archegonium. Certain of the spore-mother-cells, after the first division, show the chromosomes being transformed into the spireme of the daughter nuclei. Such figures display approximately ten short rods becoming more or less entangled with one another. Previous to the homeotypic division very definite chromosomes, unusually small and irregular in shape, were observed, but the exact number could not be determined.

IV. Discussion

The fertilization process in *Funaria flavicans* varies considerably from the processes described in the Bryophytes which have been investigated by other authors.

The mature egg of *Funaria*, at the time of insemination, is much smaller than that of any Liverwort studied. In *Sphaerocarpos* the egg is 40 x 20 μ, in *Fossombronia* it is about 25 μ in diameter, in *Riccardia* about 20 μ, whereas in *Pellia* no actual measurements are given although it is stated to be larger than that of *Riccardia*. In *Funaria* the average size of the egg at the time of insemination is 7.7 μ in diameter, a third the size of any other egg studied. The nucleus is correspondingly small. In *Sphaerocarpos* the nucleus of the mature egg is 13 x 10 μ, in *Fossombronia*, as well as *Riccardia*, it is about 10 μ, and in *Funaria* 2.9 μ, a third the size of the other nuclei. The volumes, determined from these measurements, give a much better indication of the comparative sizes of the structures studied in these different forms. These volumes are as follows:

	Egg	Nucleus
Sphaerocarpos	14,137.9 cu. μ	796.3 cu. μ
Fossombronia	8,181.9 cu. μ	523.6 cu. μ
Riccardia	4,189.0 cu. μ	523.6 cu. μ
Funaria	239.1 cu. μ	12.8 cu. μ

The relatively small size, not only of the egg but of the nucleus as well, increases the technical difficulties and may be one of the reasons that no previous cytological work has been done on the fertilization of the Mosses.

Rickett ('23) observed a quantity of mucilaginous material resulting, supposedly, from the disintegration of the ventral canal cells and the neck canal cells in *Sphaerocarpos*. This material not only filled the neck canal but also a part of the venter and was seen extruding from the neck. No such mucilaginous material was observed in the other Liverworts that have been studied, nor was it seen in *Funaria*, although an apparently similar phenomenon was observed. This will be discussed later.

The manner of the penetration of the antherozoid into the cytoplasm of the egg is dissimilar in the Bryophytes that have been studied. In *Sphaerocarpos* the membrane of the egg is very delicate and thin, and actual penetration of the antherozoid into the cytoplasm of the egg was not observed. The process is presumably instantaneous, for in eggs fixed fifteen, twenty, or forty-five minutes after insemination the antherozoid was observed as a slender curved body in the cytoplasm. The entrance of the antherozoid was not restricted to any one portion of surface of the egg. Some entered at the distal end, others at the basal end, whereas still others entered at one side.

In *Riccardia* penetration of the antherozoid is a gradual process. The antherozoid becomes applied to the surface of the egg which becomes depressed along the line of contact, and the antherozoid or its nucleus passes laterally into the cytoplasm. Material fixed twenty to thirty minutes after insemination showed the antherozoid in the surface membrane of the egg. In *Pellia* penetration is similar to that in *Riccardia*. In *Fossombronia* penetration seems to be nearly instantaneous, accompanied by a swelling of the antherozoid. In plants fixed six minutes after insemination a number of eggs was found which had been penetrated by antherozoids.

In *Funaria* the time required for penetration is somewhat longer. In material fixed one hour and thirty-five minutes after flooding only three out of seventeen eggs examined showed

partial penetration of antherozoids. However, in material killed two hours and twenty minutes after flooding all eggs showed complete penetration of the antherozoid. In *Funaria*, moreover, there is a tendency for the antherozoid to enter at the basal end of the egg, although some showed penetration at one side and a very few at the distal end of the egg. It is doubtful whether this basal end functions as a "receptive spot" as stated by Shaw ('98) in *Onoclea*. In *Onoclea* there is a definite concavity of the egg, which is not present in *Funaria*.

The length of time which the antherozoid remains in the cytoplasm is not the same for all Bryophytes that have been studied. In *Sphaerocarpos* the male nucleus remains in the cytoplasm approximately forty-six hours; in *Pellia* for about twenty-four to thirty-six hours, during which it undergoes a change in form, preparatory to nuclear fusion; in *Riccardia* it remains almost without change of form in the cytoplasm of the egg for the same length of time, after which it begins an endwise penetration of the female nucleus. In *Fossombronia* actual penetration of the male nucleus into the female nucleus was not observed. In *Funaria* the male nucleus does not remain in the cytoplasm for a long period of time, but almost immediately undergoes a change in form and position. In eggs fixed three hours and thirty minutes after flooding the male nucleus, in the majority of cases, was found to be in direct contact with the nucleus of the egg.

The greatest variation between these species exists in the methods of nuclear fusion. *Sphaerocarpos* displays the type in which the nuclei come in contact with each other, the chromatin material undergoes the formation of chromosomes, the nuclear membranes disappear, and the first division of the zygote occurs.

The penetration of the male nucleus into the female nucleus of *Fossombronia* has not been observed. The fusion nucleus shows the two masses quite distinct in the nuclear cavity.

In *Pellia* the male nucleus comes in contact with the female nucleus, whereupon the membrane of the latter disappears at the point of contact. A new membrane which is formed about the male nucleus is continuous with the female nucleus, and as a result the two nuclei are surrounded by a common membrane.

Fusion occurs, and the fusion nucleus is distinguished by the presence of two nucleoli.

In *Riccardia* the male nucleus penetrates endwise by piercing the membrane. The passage of material into the female nucleus is very slow. The two masses of chromatin are quite distinct, each occupying separate regions of the nuclear cavity, but these become optically indistinguishable before division is initiated.

The situation as described in *Funaria* offers a good many points of contrast. Penetration of the male nucleus into the female nucleus occurs very shortly after insemination. The process of penetration is similar to that in *Riccardia,* but the behavior of the two masses of chromatin is distinctly different in the two cases. In *Funaria* there is a very definite fusion of the two masses with the disappearance of the nuclear membrane. The fusion nuclear body, resulting from the coalescence of the male nucleus and the condensed reticulum of the egg, remains very distinct and definite in the central region of the egg, but is for a time not delimited by any perceptible membrane. The reappearance of the membrane some time after fusion is another point of contrast, and the fact that the chromatin material, at the inception of the prophase of the first mitosis, is distinguished at the periphery of the fusion nuclear cavity places *Funaria* in a category by itself, as far as fertilization is concerned. This particular method, distinct and unique, has not been described for any species of plant.

The fact that in all Bryophytes previously studied there is a prolonged period of time before the fusion of the two nuclei is interesting. There seems to be a very definite period in the Liverworts during which the male and female nuclei retain their identity. In *Funaria* penetration of the male nucleus into the female nucleus is followed shortly by their fusion. However, the fusion body remains in the cytoplasm of the egg for some time before mitosis occurs. Hence, the two-celled embryo is encountered in *Funaria* about the same number of hours after flooding as it is in *Sphaerocarpos.*

Rickett ('23) finds that the length of time required in *Sphaerocarpos* for visible sporophytic development is from two to eight weeks. However, in *Funaria* the length of time required for mature sporophytic development is five weeks.

The ferns, which also belong to the group of plants known as Archegoniates, have distinct methods of nuclear fusion. The processes of nuclear fusion which have been described in the ferns do not present any points of similarity to the process found in *Funaria*.

Table II represents in a condensed form the more essential points of contrast between the fertilization processes of *Funaria* and the other members of the Bryophytes which have been studied.

The presence of a mucilaginous plug in the neck of the archegonium of *Funaria* is another characteristic restricted apparently to this particular group of plants, although no other moss has been studied adequately. No record has been found of any previous mention of this plug. Rickett ('23) considers the mucilaginous material present in the cavity of the venter and the neck in *Sphaerocarpos* as analogous to the "fertilization membrane" described by other workers. The mucilaginous plug observed in *Funaria* is not comparable in structure and location with the mucilaginous material of *Sphaerocarpos,* although the latter may be similar in origin and function. In the first place, there is no indication of any such substance being present in the canal of any archegonium in which insemination has not occurred. In the second place, this mucilaginous plug is always associated with the two tiers of cells of the neck adjoining the venter, never with any other cells. In 334 archegonia examined with reference to this particular point, 219, or 65½ per cent, showed this mucilaginous plug to be present. Some of the archegonia studied were sectioned transversely; hence, if the plug were present it would not be visible in the same sections as the eggs (but the sections through that part of the neck might be expected to show it). It is entirely possible that the percentage would be much higher if all the material had been sectioned longitudinally. In all of these archegonia in which the mucilaginous plug is present it is associated with the two tiers of cells of the neck adjoining the venter. Never do any other than these two tiers of cells secrete the mucilaginous material, and hence it is inferred that this plug is a secretion of these cells but its function is as yet undetermined. If the plug were analogous to a fertili-

TABLE II

COMPARISON OF BRYOPHYTES WITH REGARD TO FERTILIZATION

	Sphaerocarpos	*Fossombronia*	*Pellia*	*Riccardia*	*Funaria*
Size of egg	40 x 20 μ	25 μ	?	25 μ	7.7 μ
Size of nucleus	13 x 10 μ	10 μ	10 μ	10 μ	2.9 μ
Penetration of male nucleus into egg	Not known	Pierces membrane	Pierces membrane	Pierces membrane	Pierces membrane
Time required for penetration	15 minutes	0–6 minutes	20–40 minutes	20–40 minutes	1 hour, 35 minutes
Penetration of male nucleus into female nucleus	No penetration, two nuclei come in contact	Not known	No penetration, fusion in reticulate condition	Endwise	Endwise
Role of nuclear membrane	Disappears	Remains	Disappears at point of contact then reappears	Remains	Disappears
Behavior of chromatin	Organized into chromosomes	Not known	Not definite	Becomes dispersed	Two bodies fuse as such
Time elapsed before fusion	44 hours	40–60 hours	24–36 hours	26–36 hours	10 hours, 30 minutes
First division of nucleus (two-celled embryo)	73 hours, 45 minutes	168 hours	144–168 hours	144–168 hours	70–93 hours

zation membrane its function would be to prevent the penetration of any supernumerary antherozoids into the egg. The presence of a relatively large number of antherozoids within the ventral cavity, after penetration of one antherozoid, makes this assumption doubtful. The fact that an unusually large number of antherozoids appears to have accumulated above the plug gives one the impression that the plug prevents further entrance of antherozoids into the cavity. It may also be conceived to afford protection against injury to the zygote, preventing evaporation of water or entrance of bacteria.

There is no indication of any fusion between the ventral canal cell and the egg cell, such as has been described by Bryan ('20) in the case of *Sphagnum*. The egg cell in *Funaria* is approximately three times the size of the ventral canal cell. The ventral canal cell, as it disintegrates, decreases in size until it is scarcely perceptible above the egg cell and then disappears completely. The rounding up of the egg cell and decrease in size of the two cells leaves a space between the two cells. This space makes it evident that the cells do not come in contact with each other, thus eliminating the possibility of fusion.

The structures observed in the cytoplasm of the egg, in the fixations which were made approximately forty-five hours after flooding, have been definitely determined to be plastids. Throughout the development of the fertilized egg, at various periods after flooding, rod-like structures and granules have been observed in the cytoplasm of the egg, but this particular lot is the only material in which definite plastids have been identified. The plastids present the same vacuolated appearance and are similar in structure to those found in other tissues of the plant except that they are smaller. Sapehin ('13) finds plastids in the egg of *Bryum*. From his drawing, however, it is very evident that the egg has just been separated from the ventral canal cell, since it does not display the definitely rounded appearance associated with mature eggs. The plastid-like bodies appear to be small, spherical, and relatively few in number. In addition to these small spherical structures Sapehin represents definite rods and minute granules. These latter structures in *Bryum* are very similar to those which are found in eggs of *Funaria* three hours and thirty minutes after insemination.

Showalter ('27b) includes a drawing of *Pellia* showing very definite starch granules. These appear in a mature egg which contains two male nuclei, but in which no nuclear fusion has occurred. Showalter ('28) has observed in eggs of *Riccardia pinguis*, type C, inseminated with antherozoids of *Riccardia pinguis*, type B, that plastids with starch grains were sometimes quite conspicuous. Motte ('28) figures very definite rods, together with some irregularly shaped bodies in the cytoplasm of the egg of *Hylocomium*. He has used the particular technique which has been developed for the study of plastids. He assumes that these irregularly shaped bodies are plastids, and considers them, inasmuch as the archegonium is advanced in age, to be plastids which develop as a result of non-fertilization of the egg and to be forerunners of cellular death. In *Funaria hygrometrica* he finds no indication of plastids in the cytoplasm of an egg that is somewhat past the mature stage.

The fixations of *Funaria flavicans* were made for other purposes than the studying of plastids, but it is interesting to note that these rod-like structures and spherical bodies are present in the cytoplasm of the egg regardless of the killing fluid or the stain used. The fluid which brought out the definite plastid bodies was that of Benda, and in other lots of material fixed in Benda's fluid no plastids, rods, or granules were observed in the cytoplasm. The rod-like structures and granules, which have been observed, are present in those eggs which show very clearly the male nucleus in contact with the female nucleus. In the later stage in which the definite plastids are observed, the presence of the mucilaginous plug would indicate that insemination had taken place. It is questionable whether nuclear fusion has occurred, since the presence of these bodies makes it somewhat difficult to determine the nuclear structure. Not all of the eggs of this particular lot show these plastids, and it is possible that they have developed because of non-fertilization. The very scanty amount of evidence prevents one from making any definite inferences regarding these plastids.

The condition of the nucleus with reference to the condensed chromatin shows some definite points of similarity to those described by Showalter ('28) for *Riccardia*. He observes that,

after penetration of the male nucleus into the cytoplasm of the egg, the chromatin of the female nucleus condenses into a compact mass about the nucleolus, leaving a region in which there is no staining substance present. In early stages the chromatin is readily distinguished about the nucleolar body. In *Funaria,* however, the region about the nucleolus is very dense in appearance and does not seem to display any of the details characteristic of true chromatin. This dense mass gradually disappears with the entrance of the male nucleus into the female nucleus, leaving a region in which there is no staining substance present. No measurements were made of the nucleolar body to determine if there was an increase in its size, which at all times is extremely minute, making detailed observations difficult. It seems logical, however, to assume that the nucleolus of the egg nucleus in *Funaria* is in reality a condensed mass of chromatin enclosing the true nucleolus and is imbedded in some cytoplasmic material which undergoes structural changes with the occurrence of fertilization.

Cytokinesis has not been thoroughly investigated in the Mosses. Wilson ('09) depicted very definitely division by cell-plate formation in *Mnium.* Allen ('16) found that the spore-mother-cell of *Catharinea* presented a lobed appearance and stated that this was the first observed occurrence of lobing in the Bryales. The lobing may be interpreted as furrows which grow in dividing the spore-mother-cell into tetrads. The method of division in *Funaria* is doubtless that of cell-plate formation. The definite thickenings which appear at the equator between the poles and which grow out toward the periphery of the cell are regarded as incipient cell-plates.

Summary

1. Sporelings, obtained from spores of *Funaria flavicans* Michx. sown on sterile soil, were grown under controlled conditions. At the time when the archegonia and antheridia were mature, insemination was brought about by flooding the cultures. Fixations were made at intervals after flooding and the material studied microscopically.

2. The volume of the egg of *Funaria* was found to be approximately one-eighteenth that of the egg of *Riccardia.* The

volume of the nucleus of *Funaria* was found to be one-fortieth that of *Riccardia*.

3. The antherozoid penetrates the cytoplasm of the egg by a gradual process, and takes place, for the most part, at the basal end.

4. The male nucleus, having assumed a spherical form, comes in contact with the female nucleus and then passes into the nuclear cavity.

5. The region about the condensed chromatin of the female nucleus is very clear, whereas the region about the male nucleus is chromophyllic.

6. After penetration of the male nucleus the nuclear membrane about the female nucleus becomes irregular in outline and disappears, leaving the condensed chromatin and the male nucleus in the center of the nuclear cavity.

7. The condensed chromatin of the female nucleus gradually fuses with the male nucleus. After this fusion has occurred, a nuclear membrane reappears around the fusion nucleus.

8. In connection with fertilization, a mucilaginous plug is developed in the neck of the archegonium. It is thought to be a secretion of the first two tiers of neck cells above the venter, since it is always found associated with these cells.

9. No fusion of the egg cell with the ventral canal cell, such as that reported in *Sphagnum* by Bryan, was observed.

10. Cytokinesis of the spore-mother-cell is by cell-plate formation.

11. These results, the only ones so far obtained in connection with fertilization in Mosses, are compared with those in other Bryophytes.

Acknowledgments

The writer wishes to express her extreme gratitude to Dr. George T. Moore for the use of the facilities of the Missouri Botanical Garden Library, to Dr. A. M. Showalter, under whose direction and guidance this problem was undertaken, to Dr. Edgar Anderson for his helpful criticisms and suggestions, and to Dr. A. J. Grout for his kindness in identifying the material used.

Bibliography

Allen, C. E. ('16). Four-lobed spore mother cells in Catharinea. Am. Jour. Bot. **3**: 456–460. 1916.

Arnell, H. W. ('75). An observation of the fecundation of Mosses. Rev. Bryol. **2**: 114–115. 1875.

Babcock, E. B., and Clausen, J. ('29). Meiosis in two species and three hybrids of Crepis and its bearing on taxonomic relationship. Univ. Calif. Publ., Agr. Sci. **2**: 401–432. 1929.

Bryan, G. S. ('20). The fusion of the ventral canal cell and egg in *Sphagnum subsecundum*. Am. Jour. Bot. **7**: 223–230. 1920.

Campbell, D. H. ('28). The structure and development of Mosses and Ferns. 3rd ed. New York, 1928.

Fry, H. J. ('30). A critique of the cytological method. Anat. Rec. **46**: 1–22. 1930.

Gayet, L. A. ('96). Recherches sur le développement de l'archégone chez les Muscinées. Ann. Sci. Nat. Bot. VIII. **3**: 161–258. 1896.

Grout, A. J. ('24). Mosses with a hand-lens. 3rd ed. New York, 1924.

Harvey-Gibson, R. J., and Miller-Brown, D. ('27). Fertilization of Bryophyta. (Preliminary note). Ann. Bot. **41**: 190–191. 1927.

Hofmeister, W. ('62). On the germination, development, and fructification of the higher Cryptogamia. Translation. London, 1862.

Van Leeuwen-Reijnvaan, W. und J. ('08a). Über eine zweifache Reduktion bei der Bildung der Geschlechtszellen und darauf folgende Befruchtung mittels zwei Spermatozoiden und über die Individualität der Chromosomen bei einigen Polytrichum-arten. Rec. Trav. Bot. Neerl. **4**: 177–220. 1908.

————, ('08 b). Über die Spermatogenese der Moose, speziell mit Berücksichtigung der Zentrosomen-und Reduktionsteilungsfragen. Ber. d. Deut. Bot. Ges. **26**: 301–309. 1908.

Motte, J. ('28). Contribution à la connaissance cytologique des Muscinées. Ann. Sci. Nat. Bot. X. **10**: 293–543. 1928.

Rickett, H. W. ('23). Fertilization in Sphaerocarpos. Ann. Bot. **37**: 225–260. 1923.

Roze, E. ('72). De la fécondation chez les Cryptogames supérieures, et en particulier chez les Sphaignes. Bull. Soc. Bot. Fr. **19**: 91–103. 1872.

Sapehin, A. A. ('13). Ein Beweis der Individualität der Plastide. Ber. d. Deut. Bot. Ges. **31**: 321–324. 1913.

Sharp, L. W. ('26). An introduction to cytology. 2nd ed. New York, 1926.

Shaw, W. R. ('98). The fertilization of Onoclea. Ann. Bot. **12**: 261–286. 1898.

Showalter, A. M. ('26). Studies in the cytology of the Anacrogynae. II. Fertilization in *Riccardia pinguis*. *Ibid.* **40**: 713–726. 1926.

————, ('27a). *Ibid.* III. Fertilization in *Fossombronia angulosa*. *Ibid.* **41**: 37–46. 1927.

————, ('27b). *Ibid.* IV. Fertilization in *Pellia Fabbroniana*. *Ibid.* 409–417. 1927.

————, ('28). *Ibid.* V. Hybrid fertilization in *Riccardia pinguis*. La Cellule. **38**: 295–348. 1928.

Vandendries, R. ('12). Le nombre des chromosomes dans la spermatogénèse des Polytrichum. *Ibid.* **28**: 257–261. 1912.

Walker, N. ('13). On abnormal cell-fusion in the archegonium, and on spermatogenesis in Polytrichum. Ann. Bot. **27**: 115–132. 1913.

Williams, R. S. ('01). *Funaria flavicans* Michx. Bryol. **4**: 9–10. 1901.

Wilson, M. ('09). On spore formation and nuclear division in *Mnium hornum*. Ann. Bot. **23**: 141–158. 1909.

———, ('11). Spermatogenesis in the Bryophyta. *Ibid.* **25**: 415–457. 1911.

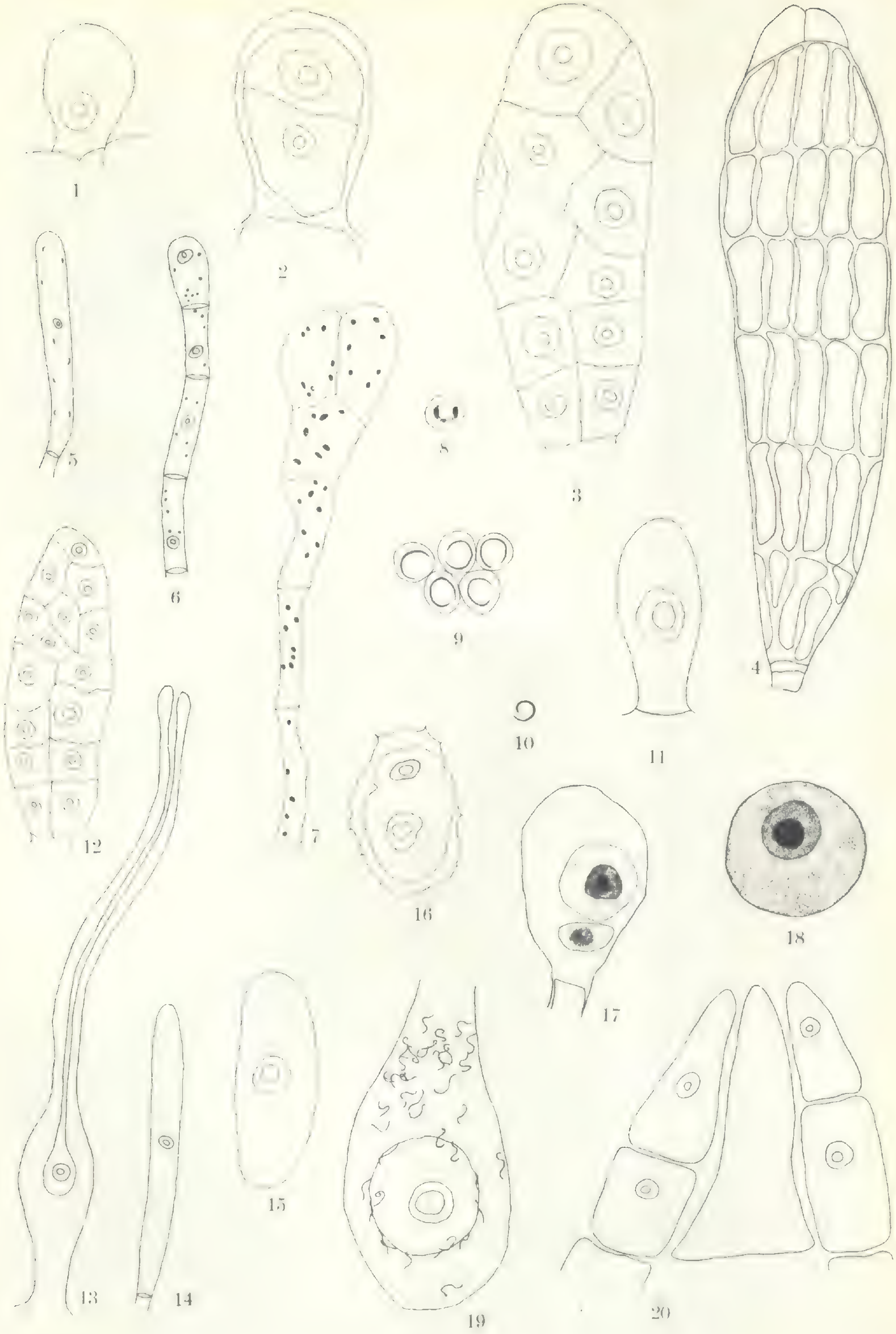
Explanation of Plate

PLATE 43

All figures were drawn with the aid of the camera lucida at the magnification indicated.

Figs. 4, 5, 6, 9, 10 were drawn from living material. Figs. 1, 2, 3, 7, 8, 11–57 were drawn from stained preparations.

Fig. 1. Single-celled antheridium. × 1500.
Fig. 2. Two-celled antheridium. × 1500.
Fig. 3. Multicellular antheridium. × 1500.
Fig. 4. Mature antheridium. × 380.
Fig. 5. Single-celled paraphysis. × 380.
Fig. 6. Several-celled paraphysis. × 380.
Fig. 7. Mature paraphysis. × 380.
Fig. 8. Intranuclear division. × 1500.
Fig. 9. Mature antherozoids in gelatinous envelope. × 750.
Fig. 10. Sperm—cilia not visible. × 750.
Fig. 11. Single-celled archegonium. × 1500.
Fig. 12. Several-celled archegonium. × 1500.
Fig. 13. Mature archegonium. × 150.
Fig. 14. Paraphysis of archegonial head. × 380.
Fig. 15. Cell before egg and ventral canal cell have been cut off. × 1500.
Fig. 16. Cell showing invagination of cytoplasm. × 750.
Fig. 17. Venter with degenerating ventral canal cell. × 750.
Fig. 18. Mature egg immediately after flooding. × 1500.
Fig. 19. Egg being surrounded by antherozoids, 35 min. after flooding. Diagrammatic × 1500.
Fig. 20. Mucilaginous plug. × 1500.



BEARDSLEY—FUNARIA FLAVICANS

AYNE, BOSTON

Explanation of Plate

PLATE 44

Fig. 21. Antherozoids adpressed to egg, 1 hr. 35 min. after flooding. × 1500.

Fig. 22. Antherozoids adpressed to egg, 2 hr. 20 min. after flooding. × 1500.

Fig. 23. Antherozoid in process of penetration, 1 hr. 35 min. after flooding. × 1500.

Fig. 24. Antherozoid in cytoplasm of egg, 2 hr. 20 min. after flooding. × 1500.

Fig. 25. Antherozoid in cytoplasm of egg, 2 hr. 20 min. after flooding. × 1500.

Fig. 26. Egg showing polyspermy, 1 hr. 35 min. after flooding. × 1500.

Fig. 27. Antherozoid assuming a spherical form, 3 hr. 30 min. after flooding. × 1500

Fig. 28. Antherozoid coming in contact with egg nucleus, 4½ hr. after flooding. × 1500.

Fig. 29. Male nucleus in contact with female nucleus, 3½ hr. after flooding. × 1500.

Fig. 30. Male nucleus in contact with female nucleus, 3½ hr. after flooding. × 1500.

Fig. 31. Male nucleus penetrating female nucleus, 4½ hr. after flooding. × 1500.

Fig. 32. Egg nucleus showing vacuolation of condensed chromatin, 4½ hr. after flooding. × 1500.

Fig. 33. Male nucleus within female nuclear membrane, 4½ hr. after flooding. × 1500.

Fig. 34. Male nucleus within female nuclear membrane, 4½ hr. after flooding. × 1500.

Fig. 35. Egg showing rod-like bodies in cytoplasm, 2 hr. 20 min. after flooding. × 1500.

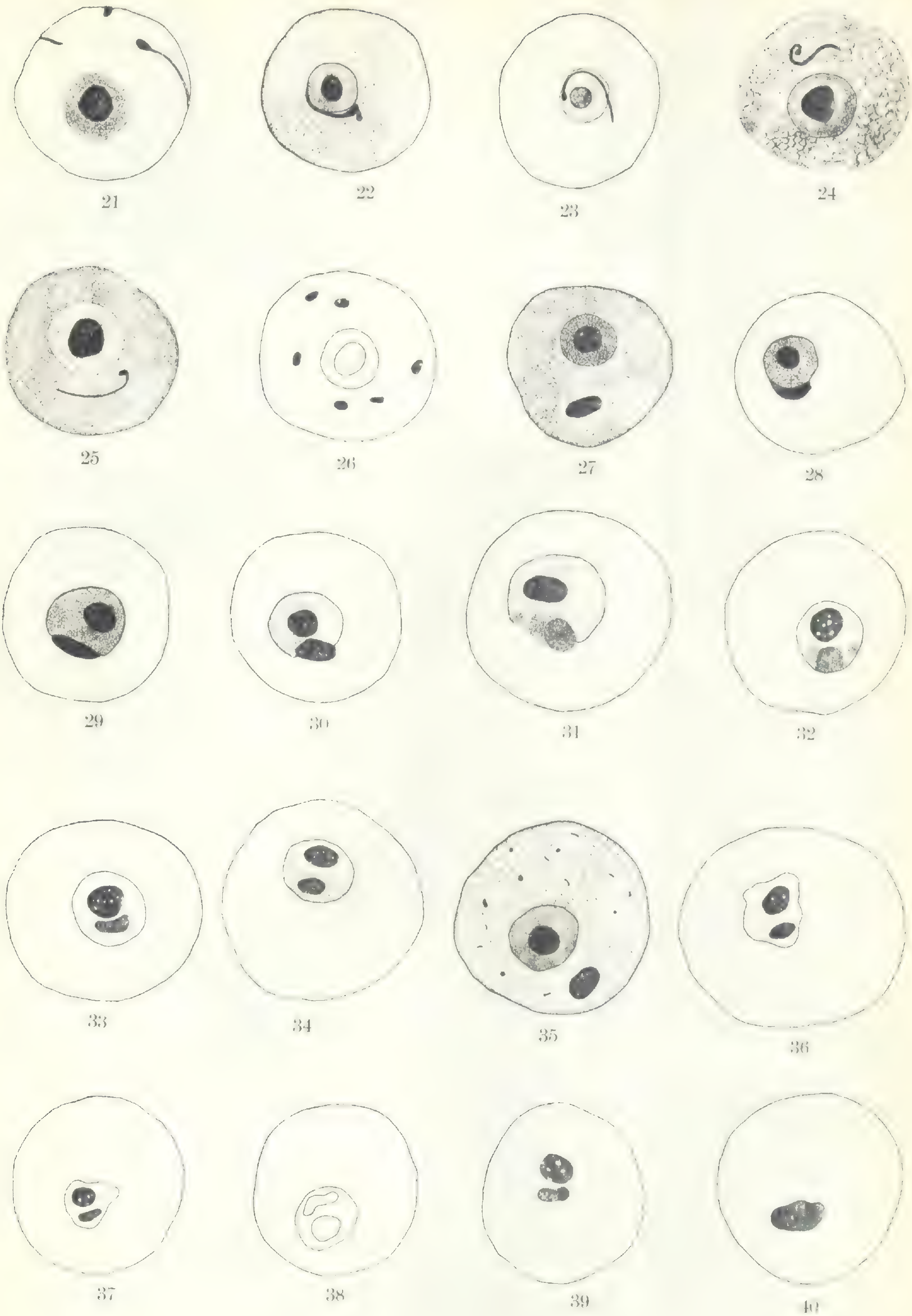
Fig. 36. Membrane becoming irregular, 5½ hr. after flooding. × 1500.

Fig. 37. Membrane becoming irregular, 5½ hr. after flooding. × 1500.

Fig. 38. Membrane becoming irregular, 6½ hr. after flooding. × 1500.

Fig. 39. Disappearance of membrane, 6½ hr. after flooding. × 1500.

Fig. 40. Maternal and paternal chromatin in process of fusion, 6½ hr. after flooding. × 1500.

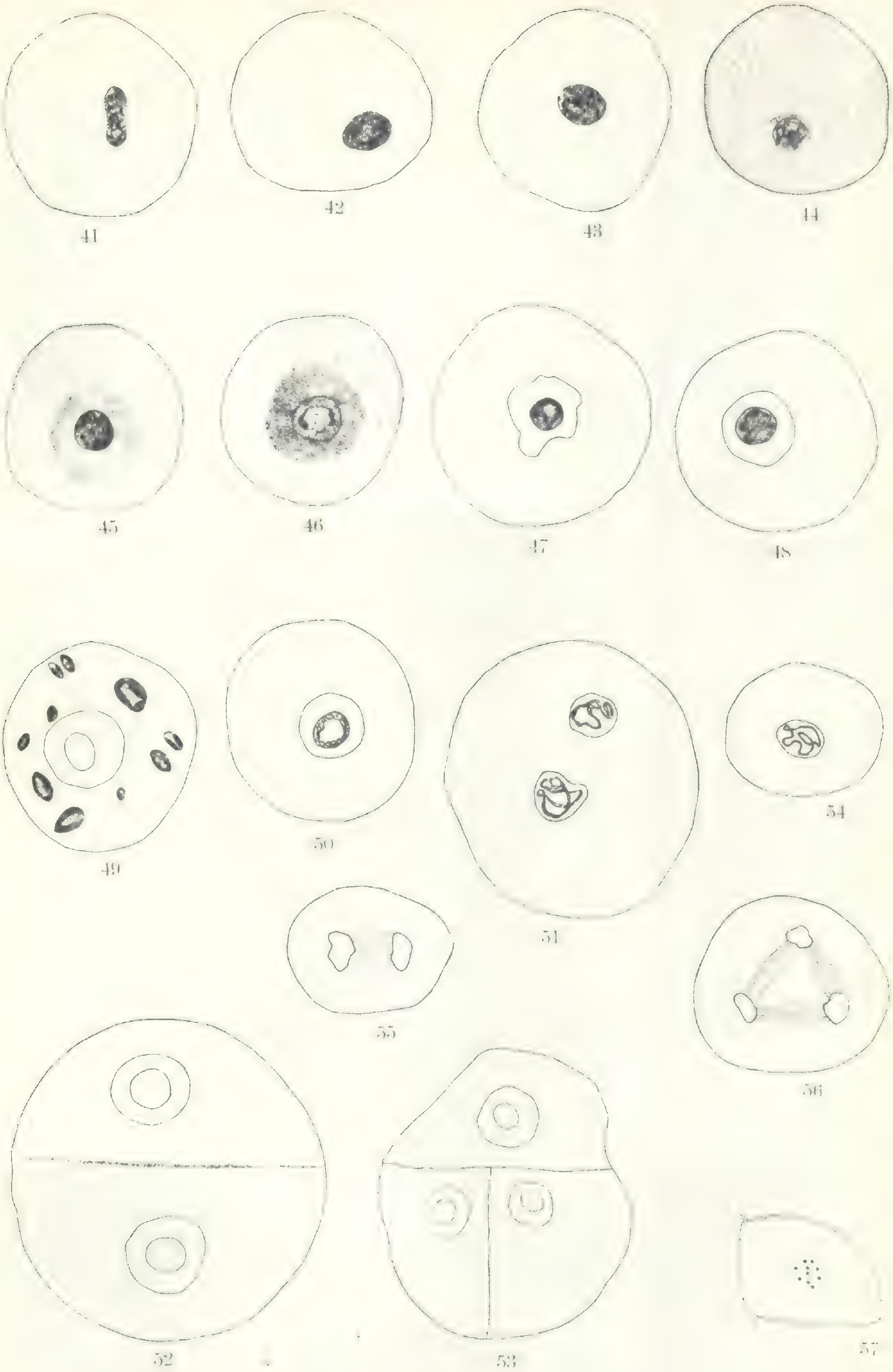


BEARDSLEY—FUNARIA FLAVICANS

Explanation of Plate

PLATE 45

Fig. 41. Maternal and paternal chromatin in process of fusion, 7½ hr. after flooding. × 1500.
Fig. 42. Fusion body, 14 hr. after flooding. × 1500.
Fig. 43. Fusion body, 14 hr. after flooding. × 1500.
Fig. 44. Cytoplasm becoming dense around fusion body, 14 hr. after flooding. × 1500.
Fig. 45. Cytoplasm denser, 16 hr. after flooding. × 1500.
Fig. 46. Cytoplasm denser, 18 hr. after flooding. × 1500.
Fig. 47. Irregular membrane, 22 hr. 20 min. after flooding. × 1500.
Fig. 48. Definite membrane, 48 hr. 45 min. after flooding. × 1500.
Fig. 49. Egg showing presence of plastids, 45 hr. 20 min. after flooding. × 1500.
Fig. 50. Egg showing dispersal of chromatin about periphery of fusion body, 93 hr. after flooding. × 1500.
Fig. 51. Binucleate embryo, 93 hr. after flooding. × 1500.
Fig. 52. Embryo showing nuclei in resting stage, 93 hr. after flooding. × 1500.
Fig. 53. Three-celled embryo, 93 hr. after flooding. × 750.
Fig. 54. Spore-mother-cell. × 1500.
Fig. 55. Spore-mother-cell during first division. × 1500.
Fig. 56. Spore-mother-cell during second division. × 1500.
Fig. 57. Chromosomes in archegonium. × 1500.



BEARDSLEY—FUNARIA FLAVICANS

NEW OR OTHERWISE NOTEWORTHY APOCYNACEAE OF TROPICAL AMERICA

ROBERT E. WOODSON, JR.

Research Assistant, Missouri Botanical Garden

Instructor in Botany, Henry Shaw School of Botany of Washington University

Tabernaemontana Killipii Woodson, sp. nov., arborea ca. 4–5 m. alta; ramulis dichotome divisis teretibus in sicco obscure angulatis junioribus brevissime scabro-hirtellis tandem glabratis; foliis oppositis petiolatis subcoriaceis late ovato-ellipticis apice breviter obtuseque acuminatis basi obtusis 25–30 cm. longis 14–15 cm. latis omnino glabris; petiolis ca. 1 cm. longis basi imo fossatis marginibus linea transversali conjunctis; cymis lateralibus divergenter dichotome ramosis 20–30-floris pedunculo scabro-hirtello 5–6 cm. longo; bracteis ovato-reniformibus scariaceis margine ciliolatis ca. 0.1 cm. longis; pedicellis 0.75–1.0 cm. longis glaberrimis; calycis lobis ovato-oblongis obtusiusculis plus minusve inaequalibus 0.3–0.4 cm. longis glaberrimis; corollae lobis oblique oblongis paulo dolabriformibus ca. 0.3–0.4 cm. longis tubo cylindrico 0.75–1.0 cm. longo; antheris linearibus omnino insertis; ovariis oblongoideis glabris nectario nullo vel vix manifesto; folliculis laevibus oblongo-ellipsoideis utrinque acuminatis divergentibus parvulis.—"Peru, Dept. Loreto: Iquitos, woods, alt. about 100 m., Aug. 2–8, 1929." *E. P. Killip & A. C. Smith 27414* (Mo. Bot. Garden Herbarium, TYPE, U. S. National Herbarium, duplicate).

Tabernaemontana Killipii is closely allied to *T. hirtula* Mart. The leaves of the former, however, are much larger, of a different shape, and with a petiole scarcely one-half the length of that of the latter species. Moreover, the inflorescence of *T. Killipii* differs from that of *T. hirtula* in having a peduncle of greater length, longer pedicels, and glabrous calyx-lobes.

Rauwolfia lauretiana Woodson, sp. nov., arborea omnino glabra altitudine ignota; ramulis teretibus cortice griseis longitudinaliter striatis sparse lenticellosis; foliis membranaceis longiuscule petiolatis ternatim vel quaternatim in apicibus ramulorum verti-

Issued December 24, 1931.

cillatis ovatis apice longe obtuseque acuminatis basi subiter attenuatis conspicue inaequalibus maioribus 9–10 cm. longis ca. 5 cm. latis minoribus 5–7 cm. longis 3.0–3.5 cm. latis petiolo 1.5–2.0 cm. longo eglanduloso; cymis terminalibus 4–12-floris divergentibus pedunculo ca. 1 cm. longo; bracteis squamosis minimis; pedicellis pedunculis subaequantibus; calycis lobis late deltoideis obtusissimis ca. .075 cm. longis 0.2–0.25 cm. latis margine minute ciliolatis intus eglandulosis; corollae tubo cylindrico basi haud dilatato ca. 1 cm. longo fauce ca. 0.2 cm. diametro extus glabro intus sub staminibus sparse piloso lobis obovatis obtusiusculis ca. 0.5 cm. longis; antheris ovoideis ca. 0.2 cm. longis apice haud appendiculatis; ovariis oblongoideis glabris nectarium annuliforme apice integrum ca. triplo superantibus; fructibus ignotis.—"Peru, Dept. Loreto: Mishuyacu, near Iquitos, alt. 100 meters; forest, Nov., 1929." *G. Klug 35* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Taking Markgraf's recent revision of the genus *Rauwolfia*[1] as a guide, it has been ascertained that *R. lauretiana* should be classified as included within the section *Grandiflorae* Mgf., and is evidently most closely related to *R. paucifolia* A. DC. From that species, however, *R. lauretiana* presents a strong contrast by reason of the leaves, which are lanceolate, 2.5–4.5 cm. long, with a petiole about 0.5 cm. long in the former species, and are ovate, 5–10 cm. long, and borne upon a petiole 1.5–2.0 cm. long in the latter. The dimensions of the floral organs are also different, the calyx-lobes of *R. paucifolia* being lanceolate, and those of *R. lauretiana* extremely depressed-deltoid. The corolla tube of the latter species, moreover, is nearly one-third longer than that of the former.

Rauwolfia sanctorum Woodson, sp. nov., arborea omnino glabra ca. 3–4 m. alta; ramis pendulis teretibus rimosis olivaceo-griseis; foliis petiolatis subcoriaceis ternato-verticillatis paene inaequalibus elliptico-oblanceolatis apice longe et acute acuminatis basi in petiolum eglandulosum 1.0–1.5 cm. longum cuneato-angustatis cum petiolo 9–14 cm. longis 3.5–4.0 cm. latis supra

[1] Mgf. in Fedde, Repert. **20**: 114–122. 1924.

nitidulis subtus pallidioribus nervis secundariis utrimque prominulis arcuatis sat remotis; cymis solitariis evidenter terminalibus dichasialibus divergentibus 8–12-floris pedunculo gracili ca. 5 cm. longo; pedicellis ca. 0.5 cm. longis; bracteis squamosis subulatis minimis; calycis lobis ovatis breviter acuminatis ca. 0.1 cm. longis vix aequalibus; corollae gilvae tubo longe cylindrico 1.25–1.5 cm. longo 0.15 cm. diametro metiente sub fauce paulum inflato extus glabro intus in dilatatione superiore barbato-piloso lobis obovato-oblongis obtusissimis ca. 0.4 cm. longis; antheris ovoideis longe acuminatis subsessilibus; stigmate late tympaniformi ca. 0.1 cm. alto apice obtuse bilobato basi annulo conspicuo ornato; ovariis obovoideis glabris nectarium breviter cylindricum duplo superantibus; fructibus ignotis.—"Colombia, Dept. Santander: northern slope of Mesa de los Santos; alt. 1000–1500 m., Dec. 11–15, 1926." *E. P. Killip & A. C. Smith 15392* (Mo. Bot. Garden Herbarium, TYPE, U. S. National Herbarium, duplicate).

Like the species immediately preceding, *Rauwolfia sanctorum* appears to be most definitely related to the species of the section *Grandiflorae*. It is a small tree bearing ternately verticillate, elliptic-oblanceolate, definitely petiolate leaves of a somewhat leathery texture. The calyx-lobes are one-twelfth to one-fifteenth the length of the corolla-tube, which is 1.25–1.5 cm. long. The terminal cyme is solitary. On the other hand, the leaves of *R. bahiensis* A. DC., which is evidently its nearest affinity, are obovate, the calyx-lobes are about one-third the length of the corolla-tube, which is only about 0.8 cm. long, and the terminal cymes are geminate or ternate. The geographical distribution of either species is also distinct.

Dipladenia Achrestogyne Woodson, sp. nov., suffruticosa volubilis pauce ramosa omnino glabra; ramis gracilibus teretibus in sicco plus minusve striatis; foliis oppositis petiolatis membranaceis late ovato-oblongis apice breviter acuminatis basi obtusiusculis 5–9 cm. longis 2.5–6.0 cm. latis in sicco fuscis subtus in parenchymate inter venulas levissimis pallidis; racemis alternatis lateralibus subterminalibusve subspiciformibus ca. 5–15-floris pedunculo foliis fere semper aequante; bracteis scariaceis ovato-lanceolatis 0.5–0.7 cm. longis pedicellos paulo superantibus; lobis calycis

scariaceis anguste lanceolatis acutiusculis 0.3–0.4 cm. longis basi intus multiglandulosis; corollae lobis oblique oblongis plus minusve dolabriformibus 0.75–1.0 cm. longis paulo reflexis tubo longe-cylindrico 1.5–1.75 cm. longo; ovariis oblongoideis glabris nectario 2–5-lobo vix manifesto; folliculis ignotis.—"Colombia, Dept. Cundinamarca: rocky canon, Chapinero, near Bogota, alt. 2800–2900 m., Sept. 18–23, 1917." *F. W. Pennell 2034* (N. Y. Bot. Garden Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Dipladenia Achrestogyne is easily distinguished from *D. congesta*, which should evidently be regarded as its closest affinity, since it is absolutely glabrous in all parts, whereas the latter species is softly tomentulose to hirtellous throughout. The inflorescence of the former, moreover, is a regular, subspiciform raceme with pedicels rather laxly and distantly arranged, differing markedly from the distally congested inflorescence of *D. congesta.*

D. Achrestogyne has been named from the Greek ἄχρηστος and γυνή, with reference to the extreme reduction of the gynoecial nectaries and to the theory that they may be regarded as carpellodes.

Dipladenia oblongifolia Woodson, sp. nov., suffruticosa volubilis plus minusve ramosa; ramis gracilibus flexuosis glabris; foliis oppositis petiolatis membranaceis late oblongis apice breviter acuminatis basi obtusiusculis 7–15 cm. longis 2.0–3.5 cm. latis supra glabris subtus tenuissime puberulis petiolo 2–3 cm. longo in annulo obscuro stipularum instructo; racemis lateralibus alternatis 3–5-floris pedunculo foliis subaequante; bracteis scariaceis minimis; pedicellis ca. 1 cm. longis; calycis lobis scariaceis anguste lanceolatis 0.5–0.7 cm. longis basi intus multiglandulosis; corollae lobis obovatis dolabriformibusque ca. 3.5 cm. longis paulo reflexis tubo 4.0–4.5 cm. longo usque 1/3 longitudinem anguste cylindrico dein latius cylindrico-dilatato fauce ca. 1.25 cm. lato; nectario 2-lobo ovariis bis vel ter breviore; folliculis ignotis.—"Bolivia, Sur-Yungas: La Florida, vec. de Yanocochi, alt. 1700 m., Dec. 6, 1906." *O. Buchtien 590* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Dipladenia oblongifolia finds its natural alliance with the group of species centering about *D. Martiana*, because of its volubile habit and conspicuous nodal, or stipular appendages. It may easily be distinguished from *D. glabra* Rusby, of the same general region of South America, by its characteristically oblong foliage which is softly puberulent beneath, and by its larger flowers which are also of a somewhat different construction in general. The squamellae, or internal glandular emergences of the calyx, moreover, are decidedly fewer in the latter species, and are arranged in groups alternate with the lobes of the calyx, whereas they are more numerous and are uniformly distributed in *D. oblongifolia.*

Dipladenia upatae Woodson, sp. nov., suffruticosa volubilis pauce ramosa omnino glabra; ramis gracilibus flexuosis in sicco plus minusve striatis; foliis oppositis petiolatis membranaceis oblongo-lanceolatis apice acuminatis basi late cordatis evidenter conduplicativis 7–12 cm. longis 2.0–3.5 cm. latis petiolo 0.5–0.75 cm. longo in annulo obscuro stipularum instructo; racemis lateralibus alternatis ca. 3-floris pedunculo foliis subaequante; bracteis scariaceis minimis; pedicellis ca. 0.5 cm. longis; calycis lobis scariaceis glabris lanceolatis acuminatis 0.4–0.5 cm. longis basi intus biglandulosis; corollae lobis late obovato-dolabriformibus ca. 2.5 cm. longis paulo reflexis tubo 2.5–3.0 cm. longo usque 1/2 longitudinem anguste cylindrico dein paulo latiore fauce ca. 0.5 cm. diametro; nectario 2-lobo ovariis oblongoideis glabris bis vel ter breviore; folliculis ignotis.—"Venezuela: Upata," date lacking, *E. Osta 1014* (Herbarium Mus. Hist. Nat. Vindobonensis, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

D. upatae falls naturally into the group of species of *Dipladenia* comprising *D. fragrans* A. DC., *D. urophylla* Hook., and *D. surinamensis* Pulle, all of which are characterized by leaves which are more or less conduplicate when desiccated. From all the close relatives to which reference has been made, however, *D. upatae* differs by reason of the extremely narrow, cylindrical corolla-throat, and in the paired squamellae, or internal calycine emergences, which are indefinite in number among the allied species.

Odontadenia cognata (Stadelm.) Woodson, n. comb.
Echites cognata Stadelm. Flora **24:** I Beibl. 79. 1841.
Anisolobus cognatus (Stadelm.) Muell.-Arg. in Martius, Fl. Bras. **6**[1]: 113. 1860.

Odontadenia Perrottetii (A. DC.) Woodson, n. comb.
Anisolobus Perrottetii (A. DC.) in DC. Prodr. **8:** 395. 1844.

Odontadenia polyneura (Urb.) Woodson, n. comb.
Rhabdadenia polyneura Urb. Symb. Ant. **7:** 337. 1912.

Odontadenia Killipii Woodson, sp. nov., fruticosa volubilis omnino glabra; ramis ramulisque teretibus fuscis lenticellas parvas conspicue gerentibus; foliis oppositis longiuscule petiolatis subcoriaceis in sicco fuscis late oblongo-ellipticis apice subiter et obtuse acuminatis basi acutiusculis 6–8 cm. longis 3–5 cm. latis petiolo 1.0–1.5 cm. longo in annulo obscuro stipularum instructo; cymis terminalibus 15–20-floris pedunculo petiolos 5–6-plo superante; bracteis ovatis squamosis 0.2–0.3 cm. longis; pedicellis 0.5–0.7 cm. longis; calycis lobis plus minusve inaequalibus ovatis vel late ovato-oblongis 0.2–0.3 cm. longis intus in marginibus positis 1–2 glandulis; corollae speciosae lobis oblique obovatis dolabriformibus 2.5–3.0 cm. longis paulo reflexis tubo 3.0–3.5 cm. longo usque 1/4 altitudinem anguste cylindrico dein staminigero et abrupte conico-dilatato; antheris linearibus dorso minute puberulo-papillatis 0.3–0.4 cm. longis; nectario tubuloso-cupuliformi apice integro vel minutissime crenulato ovariis oblongoideis glabris paulo breviore; folliculis ignotis.—"Peru, Dept. Loreto: Iquitos; woods, alt. about 100 m., Sept. 26, 1929." *E. P. Killip & A. C. Smith 29847* (Mo. Bot. Garden Herbarium, TYPE, U. S. National Herbarium, duplicate).

Odontadenia Killipii bears a strong superficial resemblance to *O. cognata*, chiefly because both species have a terminal inflorescence and foliage which assumes a decided bronze coloration upon desiccation. The coloration of the desiccated foliage, incidentally, appears to be a trustworthy and quickly perceived indicator of relationship among the species of the genus, although it has evidently never been used as such in publication. *O.*

Killipii may easily be distinguished from *O. cognata,* since the former has a corolla-tube 3.0–3.5 cm. long, narrowly cylindrical for one-quarter its length and then abruptly and broadly conical, calyx-lobes which are among the shortest of the genus, only 0.2–0.3 cm. long, and oblong-elliptic leaves which are acute or somewhat obtuse at the base; whereas the latter has a corolla-tube 5–6 cm. long, narrowly cylindrical for about one-half its length and then abruptly dilated into a much broader, cylindrical throat, calyx-lobes 0.8–0.9 cm. long, and broadly ovate-cordate leaves with a broadly auriculate base.

Odontadenia Sandwithiana Woodson, sp. nov., fruticosa volubilis omnino glabra; ramis ramulisque teretibus plus minusve longitudinaliter striatis lenticellas parvas conspicue gerentibus; foliis oppositis longiuscule petiolatis subcoriaceis in sicco olivaceis oblongo-ellipticis apice breviter et saepius obtuse acuminatis basi acutis et paulo inaequilateralibus 10–15 cm. longis 4–6 cm. latis superne angustiore petiolo 1.5–2.0 cm. longo in annulo obscuro stipularum instructo; cymis lateralibus vel pseudoterminalibus 6–10-floris pedunculo petiolos ca. duplo superante; bracteis ovatis squamosis 0.1–0.2 cm. longis; pedicellis 0.2–0.3 cm. longis; calycis lobis oblongis obtusis distinctissime inaequalibus 1.0–1.5 cm. longis intus in marginibus positis 1–2 glandulis; corollae lobis late et oblique oblongis in alabastro ca. 1 cm. longis tubo ca. 2 cm. longo usque 1/2 altitudinem anguste cylindrico dein staminigero et paulo ampliore cylindrico-dilatato; antheris linearibus dorso glabris vel minutissime papillatis 0.5–0.6 cm. longis; nectario tubuloso apice crenulato ovarium oblongoideum glabrum paulo superante; folliculis ignotis.—"British Guiana, Essequibo River: Moraballi Creek, near Bartica, alt. near sea-level, Nov. 2, 1929." *N. Y. Sandwith 552* (Herbarium Kew., TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Odontadenia Sandwithiana is closely allied to *O. Perrottetii,* indigenous to the same general region, but differs from the latter in its axillary or pseudoterminal inflorescence, its smaller corolla with a cylindrical, not campanulate, proper throat, and in its much larger leaves borne upon a petiole more than twice as long as that of the latter species. Although fully mature flowers were

not available for study, buds which were collected shortly before unfolding are of dimensions unusually small for the genus.

Odontadenia stemmadeniaefolia Woodson, sp. nov., fruticosa volubilis; ramis teretibus longitudinaliter striatis glabris in sicco dilute flavo-coloratis; foliis oppositis breviuscule petiolatis rigidule membranaceis vel subcoriaceis fuscentibus oblongo-obovatis basi saepissime plus minusve cuneato-angustatis apice breviter et obtuse cuspidatis 15–20 cm. longis 8–10 cm. latis superne angustioribus omnino glabriusculis petiolo 1.0–1.5 cm. longo in annulo obscuro stipularum instructo; cymis lateralibus 3–5-floris pedunculo foliis paulo breviore; bracteis squamosis minimis; pedicellis 1.0–1.25 cm. longis glabris; calycis lobis subaequalibus ovato-reniformibus ca. 0.2 cm. longis glabris vel margine minutissime ciliolatis intus in margine positis 2–3 glandulis; corollae lobis oblique et late obovatis 1.5–2.0 cm. longis tubo ca. 1.5 cm. longo extra calycem ventricoso-dilatato dein constricto et ad basin partis iterum dilatatae staminigero et sensim obconico-dilatato; antheris anguste oblanceolatis dorso dense lanulosis ca. 0.8 cm. longis; ovariis ovoideis glabris nectario cupulato apice crenulato et multifido subaequante; folliculis ignotis.—"Peru, Dept. Loreto: Mishuyacu, near Iquitos, alt. 100 m.; forest, Jan., 1930." *G. Klug 782* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

The nearest relative of the preceding species is evidently *O. speciosa* Benth., as is witnessed by the large, obovate and somewhat cuneate foliage and the short, obconic corolla-throat. The corolla of *O. stemmadeniaefolia*, however, is only about one-half to one-third the size of that of *O. speciosa*, and also differs in the color, which is said by the collector to have been "brick red." Additional features which may be cited as distinguishing *O. stemmadeniaefolia* from *O. speciosa* are the smaller, more nearly isophyllous calyx and the fewer-flowered inflorescence with the pedicels congested at the end of the longer peduncle. The specific name refers to the resemblance of the foliage to that of several species of *Stemmadenia*.

Odontadenia augusta Woodson, sp. nov., fruticosa volubilis; ramis teretibus lenticellas parvas conspicue gerentibus glabris

in sicco rubidulo-coloratis; foliis oppositis longiuscule petiolatis rigidule membranaceis late oblongis apice breviter et obtuse acuminatis basi obtusis superne acutiusculis 20–25 cm. longis, 8–10 cm. latis omnino glabriusculis supra fuscentibus subtus olivaceo-viridibus petiolo ca. 2 cm. longo minute hispidulo in annulo obscuro stipularum instructo; paniculis lateralibus 15–20-floris pedunculo foliis paulo breviore minute ferrugineo puberulo; bracteis ovatis squamosis minimis; pedicellis 1.0–1.25 cm. longis sicut ad pedunculos vestitis; calycis laciniis valde inaequalibus late oblongis obtusis 0.8–1.0 cm. longis extus plus minusve ferrugineo-papillatis margine ciliolatis intus in margine uniglandulosis; corollae lobis oblique et late obovato-reniformibus 1.0–1.25 cm. longis paulo reflexis tubo 4.0–4.5 cm. longo usque ⅓ altitudinem anguste cylindrico dein staminigero et sensim cylindrico-conico-dilatato; antheris linearis ca. 0.5 cm. longis dorso minute papillato-striatis; ovariis ovoideis minutissime papillatis nectarium cupulatum apice crenulatum paulo superantibus; folliculis ignotis.—"Peru, Dept. Loreto: Mishuyacu, near Iquitos, alt. 100 m.; forest, Dec., 1929." *G. Klug 657* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Although closely allied to *Odontadenia Cururu* (Mart.) K. Sch., *O. augusta* is distinct because of its much larger leaves, its longer, oblong calyx-lobes, and, particularly, the very shallow, annular nectary which does not conceal the ovary as in the former species.

Odontadenia affinis Woodson, sp. nov., fruticosa volubilis; ramis teretibus longitudinaliter striatis glabris lenticellas parvas paucas gerentibus in sicco rubidulo-coloratis; foliis oppositis breviter petiolatis subcoriaceis oblongo-ovatis apice breviter et obtuse cuspidatis basi acutiusculis 6–8 cm. longis 3.5–4.0 cm. latis omnino glabris supra fuscentibus subtus olivaceo-viridibus venis transversis prominulis petiolo 0.5–0.75 cm. longo in annulo obscuro stipularum cincto; paniculis lateralibus paucifloris breviuscule (3–4 cm.) pedunculatis; bracteis squamosis minimis; pedicellis glabris ca. 0.5 cm. longis; calycis laciniis ovatis obtusiusculis plus minusve conspicue inaequalibus 0.4–0.5 cm. longis extus glabris vel margine minutissime ciliolatis intus in margine

positis 3–4 glandulis; corollae lobis oblique obovatis 1.5–2.0 cm. longis paulo reflexis tubo 3.5–4.0 cm. longo usque ½ altitudinem anguste cylindrico dein sensim longiuscule conico-dilatato dimidiam altitudinem partis angustae staminigero; antheris anguste lanceolatis ca. 0.5 cm. longis dorso minutissime papillatis; ovariis breviter ovoideis glabris nectarium cupulatum crenulatum ca. bis terve superantibus; folliculis ignotis.—"Peru, Dept. Loreto: Balsapuerto (lower Rio Huallaga basin); alt. 150–350 m.; dense forest, Aug. 28–30, 1929." *E. P. Killip & A. C. Smith 28609* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

The insertion of the stamens midway within the narrowly cylindrical corolla-throat may be interpreted as indicating a close relationship of *Odontadenia affinis* with *O. cognata*. From the latter species, however, *O. affinis* differs because of the smaller leaves and calyx-lobes, the lateral, few-flowered inflorescence, the proportionally longer corolla-tube, and the glabrous ovary about two or three times surpassing the altitude of the shallow, annular nectary.

Odontadenia glauca Woodson, sp. nov., fruticosa volubilis; ramis teretibus evidenter gracilibus longitudinaliter striatis lenticellas parvas paucas gerentibus; foliis oppositis breviter petiolatis coriaceis in sicco margine revolutis oblongo-obovatis apice breviter et acute acuminatis basi rotundatis 6.5–8.0 cm. longis, 3.5–4.5 cm. latis supra viridibus nitidis subtus glaucis venulis transversis distinctissimis petiolo 0.3–0.5 cm. longo superne breviore; paniculis subterminalibus (vel lateralibus ?) paucifloris pedunculo brevissimi petiolis subaequante; bracteis squamosis minimis; pedicellis ca. 1 cm. longis gracilibus glabris; calycis laciniis subaequalibus ovato-triangularibus acutiusculis ca. 0.1 cm. longis vix imbricatis glabris intus in margine uniglandulosis; corollae lobis oblique oblongis in alabastro 1.0–1.25 cm. longis tubo 1.5–2.0 cm. longo gracili usque ½ altitudinem cylindrico dein staminigero et anguste tubuloso-dilatato; antheris oblongo-lanceolatis acutis ca. 0.6 cm. longis dorso glabris; ovariis ovoideis glabris nectarium 5-lobatum paulo superantibus; folliculis ignotis.—"Venezuela, Amazonas Territory: Cerro Yapacana, upper Rio Orinoco; alt.

about 100 m., April, 1931." *E. G. Holt & E. R. Blake 750* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

One of the most conspicuous and natural groups of species within the genus *Odontadenia* is that which centers about *O. nitida* (Vahl) Muell.-Arg., and comprises, in addition to that species, *O. hypoglauca*, *O. coriacea*, *O. geminata*, and *O. polyneura*. To this group *O. glauca* must be added, since it possesses the shining, glaucous foliage, the narrow corolla-tube, and the barely concrescent nectaries common to all. From all the species enumerated, however, it differs because of the smaller flowers, the extremely small (0.1 cm.) lobes of the calyx, which can scarcely be described as sheathing as in all other species of the genus, and the strongly revolute margin of the leaves.

Malouetia Killipii Woodson, sp. nov., arborea erecta ca. 10–12 m. alta; ramulis gracilibus teretibus in sicco longitudinaliter striatis lenticellas parvas et remotas gerentibus; foliis oppositis brevissime petiolatis membranaceis vel subcoriaceis late ovato-lanceolatis apice longe et obtuse acuminatis basi subiter attenuatis acutisque cum petiolo ca. 0.25 cm. longo 20–25 cm. longis 6–8 cm. latis supra glabris subtus sparse et tenuissime puberulis; cymis lateralibus vel terminalibus umbellatis brevissime pedunculatis ca. 10–20-floris; pedicellis glabris 0.75–1.0 cm. longis; bracteis squamosis minimis; calycis lobis ovato-reniformibus obtusiusculis 0.1 cm. longis 0.15–0.2 cm. latis patente inaequalibus extus apice minutissime puberulo-papillatis intus in marginibus uniglandulosis; corollae lobis ovatis acutisque 0.75 cm. longis 0.5 cm. latis extus glabris intus dense puberulo-papillatis valde reflexis tubo cylindrico basi paulo dilatato ca. 1 cm. longo saepissime glabro fauce obscure 5-squamato; antheris exsertis dorso minute et dense papillatis; nectario e glandulis 5 ovoideis truncatis subliberis ovario dimidio aequante; folliculis ignotis.—"Peru, Dept. Loreto: Iquitos, woods, alt. about 100 m., Sept. 26, 1929." *E. P. Killip & A. C. Smith 29860* (Mo. Bot. Garden Herbarium, TYPE, U. S. National Herbarium, duplicate).

Until the discovery of the immediately preceding species, there had been but one *Malouetia* reported as possessing a foliar

indument. Both species are natives of the upper Amazon valley. The previously published species, *M. pubescens* Mgf., however, is apparently to be found in a slightly different territory than that of *M. Killipii,* namely the upper Rio Branco, near S. Marcos. *M. Killipii* differs from *M. pubescens* in several important particulars. In the former the leaves are ovate-lanceolate, glabrous above, sparsely and minutely puberulent beneath, the inflorescence relatively many-flowered, the pedicels 0.75–1.0 cm. long and absolutely glabrous, the calyx-lobes ovate-reniform (about twice as broad as long), the corolla-tube 1 cm. long and the lobes but 0.75 cm. long, and the anthers merely papillate dorsally. On the other hand, *M. pubescens* is described (Mgf. Notizblatt **9**: 88. 1924) as having ovate leaves which are sparsely pilose above and very densely velutinous beneath, a few-flowered inflorescence, ovate calyx-lobes (about twice as long as broad), pubescent pedicels only 0.5 cm. long, the corolla-tube 0.3 cm. long and the lobes 0.6 cm. long, and anthers which are densely hirsute dorsally.

Macropharynx spectabilis (Stadelm.) Woodson, n. comb.
Echites spectabilis Stadelm. Flora **24**: I Beibl. 44. 1841.
Elytropus spectabilis (Stadelm.) Miers, Apoc. S. Am. 116. 1878.
Macropharynx fistulosa Rusby, Mem. N. Y. Bot. Gard. **7**: 329. *t. 6*. 1927.

Prestonia agglutinata (Jacq.) Woodson, n. comb.
Echites agglutinata Jacq. Enum. Pl. Carib. 13. 1760.
Echites circinalis Sw. Prodr. 52. 1788.
Haemadictyon circinalis (Sw.) G. Don, Dict. **4**: 83. 1838.
Anechites adglutinata (Jacq.) Miers, Apoc. S. Am. 236. 1878.

Prestonia Dusenii (Malme) Woodson, n. comb.
Echites Dusenii Malme, Arkiv f. Bot. **22A**[2]: 9. 1928.

Prestonia coalita (Vell.) Woodson, n. comb.
Echites coalita Vell. Fl. Flum. 112. 1830; Icon. **3**: *t. 40*. 1827.
Rhaptocarpus coalitus (Vell.) Miers, *l. c.* 152. 1878.

The three species enumerated above, with the possible addition of a very few others whose specific validity has not been fully

established as yet, constitute a small and very natural group the generic identity of which has been brought into dispute upon several occasions. From *Echites* (*sensu strictiore*), the group of species enumerated differs in the inflorescence, which is racemose, and in the thickened annulus of the corolla orifice. *Anechites,* on the other hand, is a genus of an entirely different subfamily, namely, Plumeroideae, which can include the foregoing species under no circumstances. *Rhaptocarpus* is a genus of no morphological validity, especially founded by Miers for the inclusion of *P. coalita.*

All three species display the essential characteristics of *Prestonia,* which may be epitomized as follows: anthers bearing two parallel sporangia ventrally upon an enlarged, sterile, basally 2-pronged connective; clavuncle fusiform; calyx-lobes bearing a solitary, internal, glandular appendage; orifice of the corolla-throat constricted by a thickened annulus; leaves eglandular. The species do not possess the five internal, strap-shaped appendages attached to the corolla-tube just above the insertion of the stamens, it is true, but those appendages should not be considered with undue emphasis, as they may or may not occur among species of indubitable congenericity (cf. *P. Muelleri* Rusby and *P. Riedelii* (Muell.-Arg.) Mgf.).

It is significant that G. Don transferred *E. circinalis* Sw. to *Haemadictyon* Lindl., a genus which is almost universally considered to be synonymous with *Prestonia* R. Br. at the present time. It is interesting to find, furthermore, that Miers also recognized the affinity of the species included under his genus *Rhaptocarpus* with those of *Prestonia* (Miers, Apoc. S. Am. 151. 1878), but mistook the undeveloped fruit of the only specimen of the former which he was able to examine for a bilocular, syncarpous capsule instead of two confluent follicles in a very immature state (to the fancied resemblance of which he frankly coined the generic name!).

Prestonia portobellensis (Beurl.) Woodson, n. comb.

Echites portobellensis Beurl. Vet. Akad. Handl. Stockh. 137. 1854 (1856).

Prestonia (*Haemadictyon*) *macrocarpa* Hemsl. Biol. Cent.-Am. Bot. **2**: 311. 1881.

The material upon which Beurling based his species is represented by two specimens collected by Billberg in April, 1826, at Porto Bello, Province of Colon, Panama, "*in silvis ad littora.*" These two specimens are in an excellent state of preservation at the present time, and are deposited in the Botanical Museum at Stockholm. *Fendler 250*, cited by Hemsley as a cotype of *P. macrocarpa*, is represented by a duplicate in the herbarium of the Missouri Botanical Garden, and has been found by the writer to be identical with the specimens of Billberg. Since *Fendler 250* bears the data "Chagres, Isthmus of Panama," it is clear that the two collections were made in the same general locality. The species is apparently frequent from Guatemala to Colombia.

Prestonia velutina Woodson, sp. nov., suffruticosa volubilis pauce ramosa; ramis gracilibus flexuosis junioribus dense luteo-puberulis; foliis oppositis brevissime petiolatis membranaceis elliptico-lanceolatis apice acuminatis basi paulo attenuatis et saepissime obtusiusculis cum petiolo 5–8 cm. longis 1.5–2.5 cm. latis supra sparse puberulo-hirtellis subtus tenue luteo-velutinis; racemis axillaribus alternatis 10–15-floris pedunculo ca. 4 cm. longo breviter luteo-hirtello; bracteis subfoliaceis oblongo-ovatis parce hirtellis 0.2–0.3 cm. longis pedicellis 2–3-plo brevioribus; lobis calycis ovato-lanceolatis acuminatis subfoliaceis ca. 0.75 cm. longis extus sparse et tenue luteo-hirtellis intus glabris basi uniglandulosis; corollae lobis oblique obovatis dolabriformibus 0.5–0.75 cm. longis valde reflexis tubo anguste cylindrico 1.0–1.5 cm. longo fauce staminigero squamis linearibus exsertis ca. 0.5 cm. longis; nectario 5-lobo ca. 0.15 cm. alto ovariis oblongoideis glabris subaequante; folliculis ignotis.—"Colombia: Hondo, Aug., 1919." *Bro. Ariste-Joseph s. n.* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Prestonia velutina simulates *P. acutifolia* (Benth.) K. Sch. in the general outline of the leaves and size and disposition of the flowers. In the former, however, the calyx-lobes are much more conspicuous and subfoliaceous, and the whole plant, with the exception of the exterior of the corolla, is covered with a fine, yellowish, velutinous or hirtellous indument.

Prestonia isthmica Woodson, sp. nov., fruticosa; ramis volubilibus teretibus sat crassis longitudinaliter striatis dense luteo-hirtellis; foliis oppositis brevissime petiolatis membranaceis oblongo-obovatis apice breviter et acute acuminatis basi obtusis et obscure auriculatis 15–20 cm. longis 10–13 cm. latis supra minute et sparse strigillosis mox glabratis subtus leviter luteo-hirtellis petiolo ca. 0.3 cm. longo ut in ramis vestito; racemis bostrycino-umbelliformibus lateralibus alternatis 4–6-floris pallide luteo-hirtellis pedunculo ca. 3 cm. longo; bracteis subfoliaceis ovato-lanceolatis 1.0–1.5 cm. longis; pedicellis 0.5–0.75 cm. longis; lobis calycis ovato-lanceolatis apice longe acuminatis basi cordatis 1.5–2.0 cm. longis 0.3–0.5 cm. latis intus basi uniglandulosis; corollae tubo longe cyclindrico 3.0–3.5 cm. longo basi ca. 0.3 cm. diametro fauce staminigero appendiculato-constricto extus pallide sericeo intus hirtello haud squamuligero lobis oblique obovatis ca. 1.5 cm. longis extus intusque glabris valde reflexis; nectario e glandulis subliberis oblongoideis 0.4–0.5 cm. longis ovaria ovoidea glabra bis terve superantibus; folliculis ignotis.—"Costa Rica: between Aserri and Tarbaca, Prov. San Jose, alt. 1200–1700 m., Dec. 6, 1925." *P. C. Standley 41332* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Prestonia isthmica differs from the neighboring *P. mexicana* A. DC. because of its longer and narrower corolla-tube with glabrous lobes, its long-attenuate, cordate calyx-segments, and its broader and larger leaves. The technical distinction of greatest significance is found in the nectaries, which are ovoid-quadrate, concrescent, and barely attain the length of the carpels in the latter species, and are narrowly oblongoid, essentially separate, and about twice surpass the length of the carpels in the former.

Laubertia Sanctae-Martae (Rusby) Woodson, n. comb.
Echites Sanctae-Martae Rusby, Descr. S. Am. Pl. 85. 1920.

Laubertia Pringlei (Greenm.) Woodson, n. comb.
Streptotrachelus Pringlei Greenm. Proc. Am. Acad. **32**: 298. 1897.
Prestonia Langlassei Standl. Contr. U. S. Nat. Herb. **23**: 1159. 1924.

The genus *Laubertia*, established by A. de Candolle in 1844 with a single species, *L. Boissieri*, until recently has been perhaps the outstanding enigma of the Apocynaceae. The type species was based upon two specimens collected by Pavon in Peru and which are now deposited in the Herbier Boissier at the University of Geneva. Apparently these are the only representatives of the original collection in existence at the present time. Although adequately described by de Candolle, the genus immediately fell into disuse, probably because few subsequent collectors retraced the itinerary of Pavon until recently.

Mueller-Argoviensis did not mention the genus in any work which the present writer has been able to consult. Miers was fortunately content merely to refer to the genus in his monograph 'On the Apocynaceae of South America,' and to call Grisebach to account for using *Laubertia* as a sectional designation under *Echites* to include three species of the West Indies properly referable to *Rhabdadenia*. K. Schumann, in Engler & Prantl's 'Natürlichen Pflanzenfamilien,' was evidently without first-hand knowledge concerning *Laubertia*, placing it between the distantly related genera *Rhabdadenia* and *Mandevilla*, and keying it upon the character of a three-lobed "discus," although later correctly describing that structure as five-lobed.

Laubertia is one of the most distinct and natural genera of the subfamily Echitoideae of Apocynaceae. As in *Prestonia*, the orifice of the corolla is conspicuously thickened and the tips of the anthers are slightly exserted, but unlike that of the latter genus, the calyx is eglandular. At present, the genus consists of only three species: *L. Boissieri* in Peru, *L. Sanctae-Martae* in Colombia, and *L. Pringlei* in southern Mexico.

NEW SOUTH AMERICAN ASCLEPIADACEAE

ROBERT E. WOODSON, JR.
Research Assistant, Missouri Botanical Garden
Instructor in Botany, Henry Shaw School of Botany of Washington University

Blepharodon minimus Woodson, sp. nov., herbacea erecta plus minusve diffusa ca. 2 dm. alta; caulibus filiformibus teretibus laxe foliatis glabris vel junioribus tenuissime puberulis; foliis patentibus patulisve oppositis brevissime petiolatis anguste linearibus 3–6 cm. longis 0.1–0.2 cm. latis utrinque glabris margine tenue ciliolatis in sicco revolutis petiolo glabro ca. 0.1 cm. longo; inflorescentiis axillaribus alternatis umbelliformibus 2–3-floris omnino glabris pedunculo ca. 0.1 cm. longo; pedicellis 0.2–0.3 cm. longis; calycis lobis ovatis acutiusculis ca. 0.1 cm. longis omnino glabris basi intus in marginibus tectis 2–3-glandulosis; corollae rotatae ostio 0.1–0.2 cm. diametro lobis ovatis acutis omnino glabris ca. 0.3 cm. longis; gynostegio sessili late conico ca. 0.1 cm. alto; coronae foliolis cuculattis late oblongo-ovatis gynostegio subaequantibus; antheris trapezoideo-oblongis appendice hyalina oblonga obtusa; polliniis oblique obovoideis; caudiculis pendentibus mediocribus; retinaculo anguste rhomboideo-oblongoideo polliniis paulo minore; folliculis ignotis.—"Colombia, Dept. Tolima: 'El Convenio,' west of San Lorenzo. Open hilltop, alt. 1000–1200 m., Dec. 29–30, 1917." *F. W. Pennell 3487* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Blepharodon minimus is most closely allied to *B. suberectus* Schltr., from which it differs in having much smaller, nearly sessile leaves with ciliolate margins, a much-reduced inflorescence with extremely short peduncle and pedicels, and an entirely glabrous calyx. The two species also differ in more technical details, such as the shape and size of the corona segments, which are oblong-acuminate and slightly surpass the gynostegium in *B. suberectus,* and are broadly ovate-oblong, obtuse, and somewhat shorter than the gynostegium in *B. minimus.* An additional detail of significance in the reproductive organs is found in the shape of the retinaculum, which is ovoid in the former species and narrowly rhomboid-oblongoid in the latter.

Issued December 24, 1931.

Stephanotella Killipii Woodson, sp. nov., suffruticosa; ramis volubilibus teretibus junioribus tenuissime et sparse puberulis maturioribus glabratis; foliis oppositis petiolatis membranaceis ovato-ellipticis apice breviter et obtuse acuminatis basi obtusis 10–20 cm. longis 6–11 cm. latis supra glabris subtus tenuissime et sparse puberulis petiolo 1.5–2.0 cm. longo tenuissime puberulo in annulo obscuro stipularum instructo; cymis axillaribus alternatis 2–3-chotomis subumbelliformibus 10–20-floris pedunculo petiolos aequante vel paulo superante; bracteis scariaceis ovatis minimis; pedicellis ca. 0.5 cm. longis; calycis segmentis scariaceis oblongo-ovatis obtusiusculis 0.3 cm. longis tenuissime puberulis basi intus in marginibus uniglandulosis; corollae tubo cylindrico 0.5 cm. longo basi paulo dilatato lobis oblique ovato-oblongis 0.4–0.5 cm. longis margine tenue ciliolatis; gynostegio stipitati ca. 0.2 cm. alto obtuse rostrato; coronae foliolis connatis gynostegio adnatis et paulo breviore; antheris elongatis membrana hyalina obtusa terminatis; polliniis oblique obovoideis erectis; caudiculis mediocribus; retinaculo anguste ligulato polliniis paulo breviore; folliculis ignotis.—"Peru, Dept. Loreto: wooded banks of Rio Itaya, above Iquitos, alt. about 110 m., Sept. 17–22, 1929." *E. P. Killip & A. C. Smith 29392* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, duplicate and analytical drawings).

The genus *Stephanotella* was established in 1885 by Fournier with a single species, *S. Glaziovii*, based upon a specimen collected by Glaziou in the neighborhood of Rio de Janeiro. Fortunately, the plant was well figured and described by Fournier, for it is evidently extremely rare, as no additional species have been ascribed to the genus until the present and no specimens of the original species are to be found in any of the larger American herbaria. It is noteworthy, therefore, that a second species of the genus should have been encountered by Messrs. Killip & Smith upon the Rio Itaya, a Peruvian tributary of the upper Amazon.

A comparison of the original description and illustration of *Stephanotella Glaziovii* (Fourn. in Martius, Fl. Bras. 6^4: 326–327. *t. 96.* 1885) with the specimen collected by Killip & Smith reveals that the two are quite similar in general appearance, but

differ in both superficial and technical characteristics. The leaves of *S. Glaziovii* are described and figured as ovate-cordate, with a broad sinus, whereas those of *S. Killipii* are ovate-elliptic, with an obtuse base. Those of the former species, moreover, are described as "pilose." whereas those of the latter are always glabrous above, with a sparse and minute puberulous indument upon the lower surface of young individuals only. The leaves of the latter species, moreover, are evidently about twice the size of those of the former.

More technical differences between the two species are abundant and of almost generic importance. The interior calycine emergences or "squamellae" of *S. Killipii* are extremely small and occur separately in the axils of the calyx-lobes, but the calyx of *S. Glaziovii* is described emphatically as "*non solum in axillis sed inter sepala et corollam pluriglandulosis.*" The lobes of the corona in *S. Killipii* are completely connate and are somewhat surpassed by the rostrum of the gynostegium. The corona of *S. Glaziovii*, on the other hand, is deeply 5-cleft almost to the base, and the narrow appendices of the anthers conspicuously exceed the gynostegium. The retinaculum of either species, finally, is very distinct, that of *S. Glaziovii* being ovoid and very thick, whereas that of *S. Killipii* is merely an attenuate ligule.

Macroscepis equatorialis Woodson, sp. nov., suffruticosa; ramis volubilibus teretibus in sicco longitudinaliter striatis dense luteo-pilosis pilis dissimilibus tum brevibus simplicibus tum multo longioribus multicellularibus sicut ad petiolos pedunculos pedicellosque; foliis oppositis petiolatis membranaceis obovatis apice breviter et obtuse cuspidatis basi anguste cordatis 15–20 cm. longis 13–15 cm. latis supra sparse strigosis subtus farinulentis et longe pilosis petiolo 4–5 cm. longo in annulo obscuro stipularum instructo; inflorescentiis axillaribus alternatis umbelliformibus 6–8-floris pedunculo ca. 1 cm. longo; bracteis linearibus ca. 1.5 cm. longis viridibus dense pilosis; pedicellis ca. 0.5 cm. longis; calycis lobis scariaceis late ovatis acutis 1 cm. longis 0.75 cm. latis brevissime puberulis apice longe pilosis basi intus in marginibus uniglandulosis; corollae tubo cylindrico-campanulato 0.75 cm. longo fauce constricto et parce appendiculato ca. 0.5 cm.

diametro lobis ovatis acutiusculis 0.75 cm. longis 0.5 cm. latis extus intusque brevissime puberulis; gynostegio subsessili; coronae foliolis corollae tubo fere ad faucem et tubo stamineo adnatis omnino inclusis apice introrsum replicatis; polliniis oblongo-obovoideis pendulis; caudiculis brevioribus apice dilatatis; retinaculo oblongo leviter compresso apice rotundato basi acutiusculo polliniis multo breviore; stigmate 5-lobo in medio excavato; folliculis solitariis ovoideis basi rotundatis apice acuminatis usque ad 9 cm. longis ad 3.5 cm. crassis late 5-alatis alis ca. 0.5 cm. latis laevibus glabris.—"Ecuador, Prov. Guayas: Oil Camp between Guayaquil and Salinas, alt. 0–100 m., June 21–24, 1923." *A. S. Hitchcock 20109* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

M. equatorialis is probably most closely related to *M. barbata* S. F. Blake, from which it differs in having somewhat larger leaves of a different shape and indument, a calyx which is definitely glandular within, and a shorter corolla-tube with lobes which are not emarginate as in the latter species. In addition, the coloration of the flowers is very probably different, that of *M. equatorialis* being described as "brown" and that of *M. barbata* as "greenish . . . the lobes dark green with a narrow pale margin" by the respective collectors of the type specimens of either species.

Phaeostemma tigrina Woodson, sp. nov., suffruticosa; ramis volubilibus teretibus dense luteo-hirtellis sicut ad petiolos pedunculos et pedicellos; foliis oppositis petiolatis membranaceis ovato-cordatis apice breviter et acute acuminatis basi late auriculatis 10–12 cm. longis 7–8 cm. latis supra densissime bullato-strigillosis subtus luteo-hirtellis petiolo 3.0–3.5 cm. longo in annulo obscuro stipularum instructo; inflorescentiis axillaribus alternatis corymboso-umbelliformibus 8–10-floris pedunculo 9–10 cm. longo; bracteis scariaceis minimis; calycis lobis linearibus obtusiusculis ca. 0.5 cm. longis ca. 0.1 cm. latis luteo-hirtellis basi intus in marginibus uniglandulosis glandulis linearibus minute pilosis; corollae rotatae pulchre flavo-fulvo-reticulatae tubo breviter cylindrico-campanulato 0.3–0.4 cm. longo glabro fauce ca. 0.5 cm. diametro lobis ovatis acutis 0.7–0.8 cm. longis

0.4–0.5 cm. latis extus minute puberulo-papillatis intus glabriusculis; gynostegio subsessili; coronae foliolis tubo corollae fere aequantibus interioribus connatis gynostegio et tubo stamineo adnatis exterioribus obtuse bilobatis inferius in medio carinatis; polliniis anguste oblongo-obovoideis pendulis; caudiculis horizontalibus auriculatis; retinaculo sagittato leviter compresso apice acutiusculo basi subhastato; stigmate depresso 5-lobo ca. 0.4 cm. diametro; folliculis ignotis.—"Colombia, Dept. El Cauca: 'Caliguala,' Coconuco, cliff near Rio San Andreas, alt. 2700–3000 m., June 14–18, 1922." *F. W. Pennell 7151* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Ph. grandifolia Rusby, the only species of *Phaeostemma* previously reported from Colombia, should probably be regarded as the nearest ally of the foregoing. From *Ph. grandifolia*, *Ph. tigrina* differs in having much smaller leaves with a different indument and with much shorter petioles, shorter and much narrower calyx-lobes, and a smaller corolla of somewhat different construction. In addition, technical differences in the reproductive organs exist. The coloration of the corolla of *Ph. grandifolia* is reported as "purple-veined and finely white-spotted, corona purple" (Rusby), and that of *Ph. tigrina* as "cossack-green, veiny on cream petals, cream center" (Pennell). The "cream center" cited by Dr. Pennell is evidently equivalent to the "corona" of Dr. Rusby's plant, and both probably refer to the plane, pentagonal stigma.

Exolobus marmoreus Woodson, sp. nov., suffruticosa alte scandens; ramis ramulisque volubilibus in sicco longitudinaliter striatis laxe foliatis dense luteo-hirtellis sicut ad petiolos pedunculos et pedicellos; foliis oppositis petiolatis membranaceis ovato-oblongis apice acute acuminatis basi late cordatis 5–9 cm. longis 3.5–6.0 cm. latis supra dense strigillosis subtus molliter luteo-puberulis petiolo 2.0–2.5 cm. longo in annulo obscuro stipularum instructo; cymis corymbiformibus axillaribus alternatisque 10–15-floris pedunculo 2–3 cm. longo; pedicellis 2.0–2.5 cm. longis; calycis segmentis lanceolatis acutiusculis ca. 0.7 cm. longis 0.1–0.2 cm. latis extus laxe pilosulis intus glabris

basi in marginibus uniglandulosis; corollae rotatae lobis ovato-lanceolatis acutiusculis usque ad 1 cm. longis 0.3–0.4 cm. latis pulchre virido-marmoreis extus glabris intus papillatis basi leviter puberulis; coronae exterioris annularis depressae leviter 5-lobatae lobis minutissime puberulis; coronae interioris foliolis oblongo-spathulatis gynostegio et tubo stamineo adnatis; antherarum angulis superioribus anguste reniformibus divergentibus; polliniis oblique pyriformibus pendulis; caudiculis horizontalibus auriculatis perbrevibus; retinaculo minuto-rhomboideo polliniis fere 6-plo breviore; folliculis ignotis.—"Colombia, Dept. Norte de Santander: between Pamplonita and Chinacota, Rio Pamplonita Valley, alt. 1300–1800 m., March 17, 1927, *E. P. Killip & A. C. Smith 20748* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

From *E. patens* (Dcne.) Fourn., which is evidently the most widespread species of *Exolobus* in South America, *E. marmoreus* differs superficially by reason of its broader leaves with shorter petioles, its more floribund inflorescence, and its smaller corolla with proportionally longer calyx-lobes. Several technical differences occur in the reproductive organs, the most conspicuous of which is the shape of the anther appendages, which are obovate in *E. patens* and narrowly reniform in *E. marmoreus*. The specific name refers to the dark greenish reticulation of the cream-colored corolla-lobes.

Marsdenia lauretiana Woodson, sp. nov., suffruticosa volubilis omnino glabra; ramis teretibus sat crassis longitudinaliter striatis; foliis oppositis petiolatis subcoriaceis elliptico-obovatis apice breviter et acute acuminatis basi attenuatis acutisque 7–10 cm. longis 2.0–4.5 cm. latis petiolo ca. 1 cm. longo in annulo obscuro glandulo-appendiculato instructo; cymis lateralibus alternatis umbelliformibus 6–10-floris pedunculo ca. 0.5 cm. longo; bracteis scariaceis vix apertis; pedicellis pedunculos aequantibus vel paulo superantibus; calycis laciniis late ovato-deltoideis obtusissimis ca. 0.3 cm. longis 0.3–0.4 cm. latis extus glabris vel obscurissime papillatis intus glabris in marginibus 3–4-glandulosis margine ciliolatis; corollae carnosae plus minusve maculatae tubo breviter cylindrico fauce constricto ca. 0.4 cm. longo

basi ca. 0.3 cm. diametro extus minute et sparse papillato intus in parte infra alas antherarum sita hirtello lobis patentibus late obovatis apice rotundatis ca. 0.3 cm. longis margine ciliolatis; gynostegio breviter stipitato; filamentis staminalibus brevibus alis tenuibus membranis antherarum apice obtusis; coronae foliolis dorso staminibus adnatis basi volvatis supra acumine lato ornatis antherarum membranis dimidia breviore; polliniis obovoideis erectis; caudiculis vix brevioribus primum descendentibus dein horizontalibus; retinaculo late elliptico superiore parte subacuminato polliniis multo breviore; stigmatis rostro conoideo muriculato apice obtuso antherarum membranas paulo superante; folliculis ignotis.—"Peru, Dept. Loreto: Mishuyacu, near Iquitos, alt. 100 m., forest, Oct.–Nov., 1929." *G. Klug 477* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

When referred to the identificatory keys of Rothe's[1] revision of the genus *Marsdenia*, *M. lauretiana* is readily included within the section *Ruehssia* subsection *Mollissimae.* The species is evidently most closely related to *M. mollissima* Fourn., but strongly contrasts with it because of the complete glabrity of the vegetative parts. The leaves of *M. lauretiana*, furthermore, are elliptic-obovate and subcoriaceous, whereas those of *M. mollissima* are ovate-cordate and membranaceous. Although sufficiently similar to include them within the same subsection, the reproductive organs also differ markedly.

[1] Rothe, in Engl. Bot. Jahrb. 52: 354–434. 1915.

SOME EFFECTS OF ULTRA-VIOLET RADIATION UPON THE CALCIUM AND PHOSPHORUS CONTENT OF HIGHER PLANTS

F. LYLE WYND

Assistant in the Henry Shaw School of Botany of Washington University

AND HARRY J. FULLER

Instructor in Botany, Henry Shaw School of Botany of Washington University

I. REVIEW OF PREVIOUS WORK AND STATEMENT OF THE PROBLEM

That ultra-violet radiation exerts an accelerative effect upon calcium and phosphorus metabolism, especially the former, has been demonstrated repeatedly. Among the numerous workers who have made studies in the field are these: Steenbock and Nelson ('23), who showed that ultra-violet rays restore growth in rats deprived of fat-soluble vitamines; Orr, Holt, Wilkins, and Boone ('23), who demonstrated that ultra-violet rays cause large amounts of calcium and phosphorus to be retained in the body; Vignard, Mouriquand, Chassard and Bernheim ('23), who brought forth radiographic evidence that ultra-violet promotes the precipitation of calcium at the junctures of bone and cartilage; Clark ('23), who showed that the diffusible calcium of the blood is higher after the serum is exposed to ultra-violet radiation; Grant and Gates ('24), who found that the blood calcium of irradiated rabbits increases considerably over that of controls. Other workers in the field have been Huldschinsky, Hess, Powers, Funk, and Park ('23), the latter of whom gives an inclusive review of the literature concerning the effects of radiant energy on rickets.

The effects of a similar treatment with ultra-violet radiation upon the calcium and phosphorus content of higher plants seemed to the authors to constitute a problem in comparative physiology worthy of investigation, because thereby an additional contribution might be made to the long list of physiologic analogies between plants and animals.

In a survey of the literature concerning the effect of ultra-violet radiation upon plants, evidence of previous work upon this question has been almost entirely lacking. Indeed it seems that Beeskow ('27) has been the only investigator to report upon the effects of ultra-violet rays on the calcium and phosphorus of plants. His work, mentioned briefly at Nashville, appeared to show that rayed plants of *Zea Mays* exhibited increased calcium and phosphorus content. In the present paper the authors have attempted to present additional and more complete data concerning this particular aspect of ultra-violet physiology.

II. MATERIAL

The plant material used in this work consisted of tomatoes and cucumbers, as employed in a previous work (Fuller, '31) on the stimulatory effects of radiation from a quartz mercury vapor arc. In that work plants were rayed according to various schedules with different screens. Of these groups, one, rayed daily for five weeks with Vita-glass at one hundred inches from the arc, showed definitely accelerated growth as compared with the controls, which received no ultra-violet radiation; the rayed and control sets were designated respectively as E and A. In comparison with the controls the plants rayed under Vita-glass were nearly one-third taller at the end of the experiment, showed a slightly increased dry weight and ash content, and were in every respect extremely healthy. Dry powders of these plants were used for the analytic work which is described below.

III. METHODS

Because of the varying analytical results obtained from different procedures, the methods used in this work are described in detail, even at the risk of repeating information already present in chemical literature.

Preparation of sample.—One-gram portions of the powdered, air-dried sample were thoroughly ashed by a Fischer burner and the residue dissolved in the crucible with 2 cc. of concentrated hydrochloric acid. The contents of the crucible were then washed into a porcelain casserole with about 50 cc. of dilute hydrochloric acid (1 : 3) and evaporated to dryness on the water bath; the

residue was baked two hours in an electric oven at 120° C. to render the silica insoluble. To the residue was then added 150 cc. of dilute hydrochloric acid, after which the casserole was allowed to stand on the water bath half an hour to insure the complete dissolving of the soluble constituents. Silica was removed by filtering through a hard filter-paper. The entire silica-free filtrate prepared from each gram of air-dried sample was used in a single determination of calcium or phosphorus in order to avoid the labor of preparing exact volumetric aliquots of a single prepared solution.

Estimation of calcium.—Calcium was estimated by titration with .1 N potassium permanganate according to the method of McCrudden ('09) and Mitchell ('21). Previous experience of the authors has shown this method to be susceptible of extraordinary accuracy, the limit of which is determined largely by the accuracy with which the original samples are taken. The prepared solution from one gram of air-dried sample was transferred to a 300-cc. beaker and made up to a volume of about 200 cc. Two drops of methyl orange were added and the solution made slightly alkaline with ammonium hydroxide (1 : 1). Dilute hydrochloric acid was then added drop by drop with constant stirring until the indicator showed a faintly acid reaction. Then 10 cc. of .5 N hydrochloric acid and 10 cc. of a 2.5 per cent solution of oxalic acid were added. The mixture was boiled, and 20 cc. of a saturated solution of ammonium oxalate added slowly with constant stirring. The mixture was heated until the precipitate became sufficiently granular for filtration, then cooled, and 8 cc. of a 20 per cent solution of sodium acetate (or enough to bring the solution to an alkaline reaction) were added. After standing over night the calcium oxalate was removed by filtration and washed with hot water until free from chlorides. The filter-paper was ruptured with a stirring rod, and the residue washed with hot water into the original beaker in which the calcium oxalate was precipitated. The precipitate was dissolved by the addition of 10 cc. of sulphuric acid (1 : 1) to the hot mixture. The hot solution was titrated immediately with .1 N potassium permanganate.

Estimation of phosphorus.—Phosphorus was estimated by precipitating with molybdate and weighing as magnesium pyrophos-

phate as described in "Official and Tentative Methods of Analysis" of the Association of Official Agricultural Chemists ('24). The prepared solution from one gram of air-dried sample was made up to about 50 cc. volume with distilled water. Concentrated ammonium hydroxide was added drop by drop with constant stirring until a slight precipitate was formed. This precipitate was dissolved by a few drops of concentrated nitric acid. Since hydrochloric acid had been used as a solvent for the ash, about 15 grams of dry ammonium nitrate were added. The solution was heated, and 40 cc. of molybdate solution were added. The mixture was digested an hour on the water bath, filtered, and the residue washed with dilute ammonium nitrate. The precipitate was dissolved on the filter-paper with ammonium hydroxide (1 : 1) and the paper washed with hot water until the volume of solution and washing was about 100 cc.

Hydrochloric acid (1 : 3) was added drop by drop until only a faint odor of ammonia remained, and the solution cooled in the Kelvinator. To the chilled solution 10 cc. of magnesia mixture were added by means of a burette, drop by drop, with vigorous stirring. After 15 minutes 10 cc. of concentrated ammonium hydroxide were added, and after standing over night the precipitate was filtered on an ashless filter-paper and washed free from chlorides. It was then ignited with a Fischer burner to a constant weight of magnesium pyrophosphate.

TABLE I

STIMULATORY EFFECTS AS EXEMPLIFIED BY WEIGHT DATA

Plant	Average wet weight per plant in gms.		Average dry weight per plant in gms.		Average ash % of dry weight	
	Control A	U-V. E	Control A	U-V. E	Control A	U-V. E
Cucumber	11.75	14.16	1.059	1.423	18.02	20.29
Tomato	10.52	15.18	.8489	1.586	16.98	19.15

TABLE II

DATA ON PHOSPHORUS ANALYSES

	1		2		3	4	
Plant	% P_2O_5 of dry weight		Average uptake of P_2O_5 per plant in gms.		Average % increase of P_2O_5 per plant of the rayed plants	Average % decrease of P_2O_5 in dry weight in rayed plants	
	Control A	U–V. E	Control A	U–V. E		Actual decrease (A–E)	Relative decrease $\left(\frac{A-E}{A} \times 100\right)$
Cucumber	1.498±.034	1.385±.043	.0159	.0197	23.89	.113	7.54
Tomato	1.146±.022	.9865±.025	.0097	.0156	60.82	.159	13.87

Explanation of tables.—Column 3 represents the average per cent increase of the total uptake in grams of P_2O_5 per plant. Column 4 represents two phases of the results relative to dry weight. The first, the actual difference, represents the algebraic difference between the controls and the rayed sets; the second, the percentage of this difference.

TABLE III

DATA ON CALCIUM ANALYSES

Plant	1		2		3	4	
	% CaO of dry weight		Average uptake of CaO per plant in grams		Average % increase of CaO per plant of the rayed plants	Average % increase of CaO in dry weight	
	Control A	U-V. E	Control A	U-V. E		Actual increase (E-A)	Relative increase $\left(\frac{E-A}{A} \times 100\right)$
Cucumber	4.239±.048	4.596±.088	.0449	.0654	45.43	.357	8.44
Tomato	2.769±.022	2.824±.012	.0235	.0448	90.64	.055	1.98

IV. DISCUSSION

From the tables it is obvious that, first, the calcium content of the rayed tomato and cucumber plants is greater than that of the unrayed plants, and second, the phosphorus content of the rayed sets is lower than that of the controls. The results concerning calcium, then, support the findings of Beeskow and show an interesting similarity to the physiologic effects of ultra-violet radiation on animal tissue. As to the results of the phosphorus analyses, however, the condition is reversed—the rayed plants show the lower content, a condition contrary to that found by Beeskow and to that obtaining in animal tissue subjected to ultra-violet. The actual phosphorus *uptake* of the rayed plants is larger, however, than that of the controls, as is shown in column 3, table II, since the rayed plants show a greater amount of growth; but the actual percentage of phosphorus in the latter plants is lower than that of the controls.

No attempt is made in this paper to present an explanation of these phenomena concerning calcium and phosphorus, since data requisite to such an explanation, particularly information about phytosterol activity and vitamine potency, are lacking. The paper does, however, emphasize the definite calcium increase.

V. SUMMARY

1. Tomato and cucumber plants which had been stimulated to greater growth by ultra-violet radiation showed a definite increase in calcium content, calculated as percentage of dry weight.

2. The same plants showed a decrease in phosphorus content, determined in the same manner.

3. The analytic procedure is described in detail.

VI. ACKNOWLEDGMENTS

The authors express their gratitude to Dr. Ernest S. Reynolds, of the Henry Shaw School of Botany of Washington University, for his interest in and suggestion of the problem, and to Dr. E. O. Stafford and other members of the department of chemistry of the University of Oregon, for their invaluable suggestions concerning the analytic work and their kindness in providing excellent laboratory facilities. Thanks are also due Dr. George T. Moore,

of the Missouri Botanical Garden, for the use of the facilities of that institution.

BIBLIOGRAPHY

Association of official agricultural chemists. ('24). Official and tentative methods of analysis. ed. 2. 1924.

Beeskow, H. C. ('27). Some physiological actions of ultra-violet rays on plants. Paper at Am. Assoc. Adv. Sci. Plant Physiol. Sect. Nashville, Dec. 1927.

Clark, J. ('23). The effect of ultra-violet light on the condition of Ca in the blood. Am. Jour. Hyg. **3**: 481. 1923.

Fuller, H. J. ('31). Stimulatory effects of radiation from a quartz mercury vapour arc upon higher plants. Ann. Mo. Bot. Gard. **18**: 17–40. 1931.

Grant, J. H., and Gates, F. L. ('24). A preliminary survey of the effects of ultra-violet light on normal rabbits. Soc. Exp. Biol. and Med. Proc. **21**: 230. 1924.

McCrudden, F. H. ('09). The quantitative separation of Ca and Mg in the presence of phosphates and small amounts of iron devised especially for the analysis of foods, urine, and feces. Jour. Biol. Chem. **7**: 83–100. 1909.

Mitchell, J. H. ('21). Report on inorganic plant constituents. Assoc. Off. Agr. Chem. Jour. **4**: 391–394. 1921.

Orr, W. J., Holt, L. E. Jr., Wilkins, L., and Boone, F. H. ('23). The Ca and P metabolism in rickets with special reference to ultra-violet ray therapy. Am. Jour. Diseases of Children **26**: 362–372. 1923.

Park, E. A. ('23). The etiology of rickets. Physiol. Rev. **3**: 106. 1923.

Steenbock, H., and Nelson, E. M. ('23). Light in its relation to ophthalmia and growth. Jour. Biol. Chem. **56**: 355–373. 1923.

Vignard, Mouriquand, Chassard and Bernheim ('23). Influence des rayons ultra-violets sur la precipitation du Ca dans les os rachitques. Lyon Méd. **32**: 1021. 1923.

STUDIES OF THE EFFECTS OF DIFFERENT LENGTHS OF DAY, WITH VARIATIONS IN TEMPERATURE, ON VEGETATIVE GROWTH AND REPRODUCTION IN COTTON[1]

EARL E. BERKLEY

Research Fellow in the Henry Shaw School of Botany of Washington University[2]

Historical Review

The work of Garner and Allard ('20) has aroused considerable interest concerning the seasonal behavior of plants. These investigators have laid particular stress upon the relative lengths of day and night as factors which largely determine the vegetative and reproductive growth of plants. Adams ('20) showed further that the number of capsules formed was largely determined by the length of day. Tjebbes and Uphof ('22) showed that increased length of day hastened the germination of seeds of many cultivated plants. Harvey ('22), by using a wide range of plants, found that many cultivated plants, as well as many common weeds, could bear flowers and fruits in much less time under continuous light than with normal daylight, thus producing more than one generation in a single season. Wanser ('22) states that in winter wheat a certain length of day is necessary in order to stimulate the formation of a jointed stem following the winter rosette condition, and a still longer day for the production of flowers and fruits. Redington ('30) grew a large variety of plants under artificial light, but too few plants of each species to draw reliable conclusions.

Considerable question was raised as to the cause of these effects of light. Koningsberger ('23) suggested that the intensity of light is the effective agency rather than the length of day. Adams ('24) disproved this idea and showed that under the same intensity of light and at the same temperature different species of plants give entirely different results, some flowering with one

[1] An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of master of science in the Henry Shaw School of Botany of Washington University.

[2] A fellowship established by the American Creosoting Co.

length of day and others with an entirely different light period. Aso and Umejiro ('24), Munerati ('24), and Tinker ('24) confirmed these findings and further showed that the vegetative growth is directly proportional to the length of daylight when the temperature and other factors are equal. Adams ('25) grew a number of cultivated plants under constant illumination of 700 watts with daylight excluded, and found that the castor bean alone produced viable seeds. Three of the other plants produced normal flowers but no fruits. He suggested that temperature might in some cases compensate for reduced light.

Deats ('25) showed that tomatoes produced more flowers and set more fruits under a long day, whereas pepper set more fruits under a short day. With both species the amount and rate of vegetative growth of various parts of the plants were directly proportional to the length of day. Doroshenko ('27) enlarged on this work, showing that different varieties of the same species varied with the length of day. He showed also that in wheat, barley, and flax the decrease in length of day caused reduction in the size of the cells, reduction in size and increase in number of stomata, and an increased development of veins per unit surface area, whereas a further shortening of the length of day reversed these changes.

Johansson ('27) showed that increased intensity of illumination increased the weight of the root systems of plants in the greenhouse, and that prolonged exposure to weak light also increased the weight of the roots. Stems were similarly affected, but only at the exposure of 6 to 8 hours per day did increased light intensity stimulate leaf production. Zimmerman and Hitchcock ('29) found that in six varieties of dahlia the formation of large storage roots was correlated with a short day, and a fibrous root system with a long day. Flowering appeared to be independent of the formation of storage roots in most of the varieties used but correlated in one or two. Nitrates accumulated in the leaves of the plants exposed to the short day, but little if any in those exposed to the long day.

Garner and Allard ('27), in a preliminary report and later ('31) with more complete data, showed that with a total daily illumination of 12 hours, a progressive shortening of the periods

of alternation of light and darkness resulted in a decided decrease in growth of most plants used. The minimum was reached with light-darkness alternations of about one minute, whereas further shortening of the alternations to 15 seconds gave decided improvement in growth. The injurious effects of the intermediate alternations included apparent destruction of chlorophyll, general etiolation, localized dying of leaf tissue, reduction in leaf development and others. The effects on growth were very similar in both short- and long-day plants but flowering was promoted in the long-day plants. Other combinations of length of day were used, such as the darkening of plants for certain hours during the middle of the day.

The amount of growth and nodule development of soy beans was found by Eaton ('31) to correlate with the length of day and the degree of severity of clipping of the leaves. Nodule development was proportional to the percentage of carbohydrates which was greatly reduced by severe clipping or by a short day.

Temperature has been recognized as an important factor in the rate of growth and time of reproduction of plants. Fung ('11) measured the temperature and relative humidity conditions in which he grew cotton plants in both soil and water culture. Although he grew the plants for only a short time, he found that they were very sensitive to differences in temperature and humidity. The thermal death point was found to be about 129° F. with a relative humidity of 88 per cent. The experiment was not carried sufficiently long to make accurate determinations but he found the optimum conditions for vegetative growth for a certain variety of upland cotton to be a temperature of about 90° F. with a relative humidity of 72 per cent, whereas those for sea island and Egyptian varieties were nearer 85° F. and 70 per cent relative humidity.

Garner and Allard ('30) called attention to the fact that certain varieties of soy beans show a seasonal fluctuation in time of flowering which is correlated with seasonal fluctuations in temperature. The length of day appeared to be the determining factor in the time of flowering in different early and late varieties of soy beans, but changes in temperature either hastened or delayed the period of reproduction.

Eaton ('24) grew a number of plants in the open under a fixed period of illumination of 13 hours per day and three temperatures: 50, 65 and 90° F. during the night. He found that peking soy beans produced more than twice as much vegetative growth at low as at high temperature. The plants grown at a high temperature flowered within 21 days as compared with 45 days at low temperature. Cotton (var. durango) died immediately at the low temperature but grew well and produced a good quantity of fruits at the high temperature. The plants kept at 65° during the night grew rapidly, becoming larger than those at high temperature but did not flower until the experiment was closed. The differences in time of flowering in these sets of plants were almost as great as the differences effected by exposing to varied lengths of day.

Gilbert ('26a) grew soy beans, cosmos, salvia, cotton, and buckwheat under a constant day length, varying temperature and humidity. Flowering was retarded in cotton and soy beans by the lower temperature and higher humidity. Cosmos, on the other hand, flowered earlier under the lower temperature and higher humidity, whereas salvia and buckwheat showed no selective reaction to temperature and humidity. In this experiment the light was kept constant, but in the same year ('26b) Gilbert grew *Xanthium pennsylvanicum* under three different day lengths and varied the temperature. The different day lengths were: (1) the normal day of the winter months, from 10 to 13.1 hours light per day, continued in the spring by covering the plants at the end of the 10-hour light period; (2) a slightly longer day of 13.8 to 14.6 hours per day during the spring months; (3) continuous light. The temperature range was from 65 to 95° F. for his high-temperature plants and 42 to 88° F. for his low-temperature plants as given by average weekly minimum and maximum temperatures. As some of these plants were grown in the open (garden), they can hardly be compared with plants grown in the greenhouse. The higher temperature-short day plants showed indications of flowering 12 to 15 days after planting but few fruits were produced. The higher temperature-long day plants flowered 47 days after planting. The low temperature-short day plants produced staminate flower buds after 116 days. The

lower temperature-long day plants in three different sets showed a minimum vegetative growth before flowering of 92 days and a maximum of 197 days in respective sets. These results do not coincide exactly with the results obtained by the author on cotton, but show the importance of temperature variations in the reproduction of plants. Kellerman ('26) in his review of the discovery of photoperiodism states that cold weather may delay growth, thus delaying flowering, and hot weather may hasten it, but if the light period is not suitable weather conditions cannot cause flowering.

Atkinson as early as 1892 made some careful observations in which he noticed that the changing from one extreme to another of weather conditions caused an increased shedding of all forms in cotton. He noticed also that an excess of water as well as drouth would cause shedding. Balls ('12) in a series of experiments confirmed these observations and showed further that a disturbance of the root system or other injury might cause abscission. He found also that the bolls were shed when young more abundantly than after developing to a certain size when little or no shedding was noticed. Lloyd ('16) suggested irrigation as a possible prevention of boll shedding, as he thought it was largely due to too rapid transpiration. Coit and Hodgson ('18) stated that the June drop of navel oranges is due largely to climatic conditions, the transpiration rate being greater than the absorption rate. Thus the older fruits and leaves draw moisture from the young fruits which in turn causes them to fall. They suggested the growing of such crops as alfalfa in the orchards in order to keep a more uniform humidity.

Lloyd ('20a) found that a water deficiency was the cause of a large amount of abscission of the young fruits of *Juglans californica quercina*. He found also while working with cotton that a shower of rain on newly opened flowers caused some injury which ultimately led to abscission, and attributed the injury to a lack of pollination due to the rain. He suggested that the shedding of young bolls might be due to a competition for moisture, the older bolls robbing the younger ones in the case of a deficiency. Mason ('22) suggested that there should be a regulation of growth at or during the time of anthesis. He also observed that a low light

intensity, accompanied by low evaporation rates and day rains, is often the cause of abscission of forms. Martin and Loomis ('23) tried an irrigation experiment but failed to solve the problem, showing that there are factors other than the moisture content of the soil causing the abscission of forms in cotton. Detjen ('26) made a thorough examination of the bolls shed and found that bolls with no fertile seeds were shed immediately after flowering and were of little significance. Embryo abortion seemed to be the chief cause of the dropping of immature fruits. Namikawa ('26), working with a great variety of plants, and Dutt ('28), on the morphology of abscission in cotton, have contributed to the knowledge of the abscission of floral organs.

Methods

EXPERIMENT I

In the present investigations cotton seeds were treated either with 75 per cent H_2SO_4 or 1 per cent $HgCl_2$ for 30 minutes, after which they were thoroughly washed and soaked in tap water for 2 hours. They were then planted in a 1:6 sand and loam mixture, to which a little ground sphagnum had been added. The soil was sterilized by autoclaving for 2 hours. Most of the seeds were planted in 4–5-inch pots, but some in flats from which they were transplanted to pots while very small seedlings. While the major planting was on December 17, a few were planted three days later.

After germination the seedlings were divided into three equal groups, as follows: group 1 was grown under normal daylight, group 2 under a sixteen-hour day, and group 3 under continuous light. The normal daylight was supplemented by electric light produced by 300-watt incandescent lamps placed about 12 inches from the tops of the plants. All plants were kept as nearly as possible at the same temperature, 25 to 30° C., and all were given the same amount of water. These conditions were continued until February 3, when two distinct series were developed from the three existing sets. Series I was kept at a usual temperature of 20–24° C., while series II was kept as near as possible at 30–34° C. in another greenhouse compartment. Conditions permitting a more constant temperature would have been more desirable. Each series was subdivided twice as shown in table I, first into

divisions 1, 2 and 3, on the basis of the length of day, and second into subdivisions A and B, for different conditions of soil moisture. Subdivision A received less water than B.

TABLE I

THE ARRANGEMENT OF THE EXPERIMENTAL PLOTS BEFORE MARCH 13 AS TO THE TEMPERATURE, LIGHT, AND MOISTURE, AND THE NUMBER OF PLANTS IN EACH PLOT

	1		2		3	
	12-hour day		16-hour day		24-hour day	
	A Low Moist.	B High Moist.	A Low Moist.	B High Moist.	A Low Moist.	B High Moist.
I 20–24° C.	20 plants	20 plants	20 plants	20 plants	20 plants	20 plants
II 30–34° C.	20 plants	20 plants	20 plants	20 plants	20 plants	20 plants

The plants were grown under these conditions until March 13, when subdivision B was modified as shown in table II. The extra plants used in the new grouping were miscellaneous plants grown for the most part in ordinary daylight and a temperature of 30–34° C. Subdivision A was continued without modification until the end of the experiment except that all plants were given an equal amount of moisture after March 13, since sufficient room was not available to carry the third subdivision which would have been desirable. This change from one length of day to another was intended to show the effects of a sudden change of length of day on the growth rate and on the development of flowers and the setting of bolls. At this time (March 13) all divisions except II–3 had developed squares, some more than others.

Division 4, which was made up from I–1–B, I–2–B, I–3–B and 10 plants from a general stock, was given 8 hours light per day (table II). Division 5, which was made up from the same sources as 4 (shown in table II), was given a 4-hour day. During the dark period both 4 and 5 were kept in a common dark room which had a temperature of about 25° C. One-half of each division was

kept in the warm room and one-half in the cold room during the light period.

TABLE II

THE POSITION OF THE EXPERIMENTAL PLANTS AFTER THE CHANGES OF MARCH 13

	1		2		3		4	5
	12-hour day		16-hour day		24-hour day		8-hour day	4-hour day
	A*	B*	A	B	A	B		
I 20–24° C.	Cont.		Cont.		Cont.		(1–10) I–3–B (11–20) I–2–B	(1–10) I–2–B (11–20) I–3–B
II 30–34° C.	Cont.	(1–10) II–3–B (11–20) II–2–B	Cont.	(1–10) II–1–B (11–20) II–3–B	Cont.	(1–10) II–1–B (11–20) II–2–B	(1–10) I–1–B (11–20) Misc.	(1–10) Misc. (11–20) I–1–B

In each set indicated above, the figures in parentheses represent a group of ten plants which was changed from its original position in the series; division and subdivision of table I, indicated by the symbols below these figures.

* Previous to March 13 represented differences in moisture.

The height of each plant was taken on February 3 and 22, March 13, April 5 and 21. The squares, flowers, and bolls were counted daily, and a record was made of each form shed, the approximate age of the shed squares, and the age of the shed bolls from the time the flowers opened. The general growth habits were noted as well as other interesting features.

EXPERIMENT II

Cotton seeds of the variety Upland Big Ball were soaked in 75 per cent H_2SO_4 for ten minutes, washed thoroughly, and planted October 8 of the second year in nine-inch pots, in a rich sandy loam with a small amount of clay. The seedlings were grown at ordinary greenhouse temperature until October 22, at which time they were moved to separate compartments for the duration of the experiment.

The experimental greenhouse was divided into a number of adjacent compartments 6 x 18 feet in size, which opened out into a hallway along the west side. They were equipped with benches along both sides and across one end. These benches were 2½ feet wide along the sides and 3 feet along the end, giving ample room for the plants during the early stages of growth but crowding them somewhat towards the last. Two adjacent compartments were used, the outer one at the end of the greenhouse being for the lower-temperature plants. These compartments were steam-heated with a double coil under each bench along the side. In the higher-temperature room an extra double coil was installed to prevent a temperature drop during unusually cold nights.

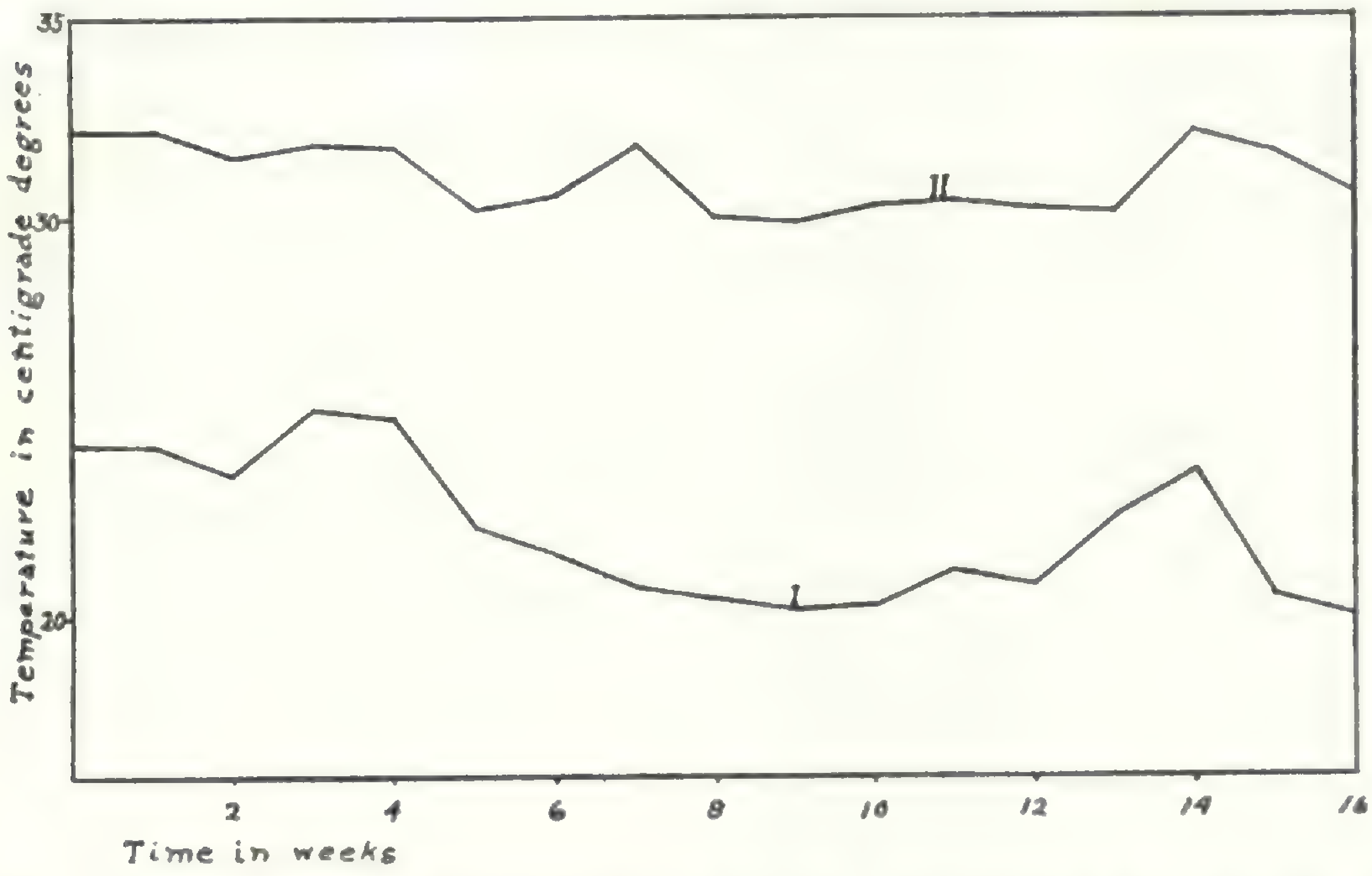


Fig. 1. Average weekly temperature of the two compartments as recorded four times daily. Compartment I, low temperature; compartment II, high temperature.

Compartment I was kept at an average temperature of 21.9° C. and compartment II at an average temperature of 30.9° C. Temperature readings were taken four times daily: 8 A.M., 1 P.M., 6 P.M., and 11 P.M. These readings were averaged into weekly temperatures as shown in fig. 1. The relative humidity was not measured but it appeared to be comparatively high most of the time, especially in the lower-temperature room.

One hundred plants were grown in each compartment. They

were divided equally into two sets A and B of 50 plants each. Set A received no light other than that of the short day of the winter months. Set B received approximately 20 hours of light each day, the daylight being supplemented by incandescent lamps of 300 watts. These lamps were arranged above the plants so as to give a good distribution of light and not affect the plants too greatly by temperature differences. A and B were separated at night by heavy canvas curtains. The curtains did not keep out all of the light but the small amount of reflected light was of low intensity.

The plants were arranged in three rows on the benches. At the time of measuring, every 14 days, they were shifted systematically as to position in order to minimize differences in the local effects on the plants of temperature, light, and humidity.

The height of each plant from the soil to the apical bud region was measured every 14 days, and the squares as developed were counted at the time of measuring. Thus an individual record of each plant was kept. The plants were harvested on February 14, at which time a record was taken of the squares present and those fallen, leaves one inch or more in diameter present and those fallen, the number of internodes, and the number of branches per plant. The plants were cut off at the ground line and the green and dry weights were determined (table vi).

Results

TOTAL GROWTH AND GROWTH RATE

Experiment I.—Cotton seeds treated for 30 minutes in 75 per cent H_2SO_4 or in 1 per cent $HgCl_2$ gave higher percentage germination than untreated seeds. The young seedlings from seeds treated in H_2SO_4 or $HgCl_2$ showed little or no signs of damping off or wilt diseases when planted in sterilized soil. They grew more rapidly and withstood the low temperature with less injury than the untreated seedlings. Some seedlings, however, showed signs of injury.

The different lengths of day and the differences in temperature were correlated with marked differences in the growth of the cotton plants. The amount of growth was proportional to the length of day when the temperature and moisture were the same

(table III and pl. 46, figs. 1 and 2). The growth rate increased with the increase in length of day.

TABLE III

THE AVERAGE HEIGHT IN INCHES OF EACH SET OF 20 PLANTS TAKEN ON THE RESPECTIVE DATES

	Date	1		2		3	
		12-hour day		16-hour day		24-hour day	
		A Low Moist. Ht.	B High Moist. Ht.	A Low Moist. Ht.	B High Moist. Ht.	A Low Moist. Ht.	B High Moist. Ht.
I 20–24° C.	February 3	8.7	8.3	10.4	11.3	11.8	12.9
	February 22	9.5	10.0	11.0	12.4	12.8	13.8
	March 13	10.7	11.0	12.5	14.0	15.0	15.0
	April 5	11.7		14.4		17.0	
	April 21	11.9		15.0		18.8	
II 30–34° C.	February 3	9.3	8.8	11.3	11.9	12.1	13.0
	February 22	11.3	11.9	13.1	16.7	15.5	18.8
	March 13	14.0	15.4	15.1	20.5	21.1	25.0
	April 5	17.5		26.5		30.8	
	April 21	19.4		30.8		34.0	

TABLE IV

THE AVERAGE HEIGHT IN INCHES OF EACH SET OF 20 PLANTS TAKEN ON THE RESPECTIVE DATES, AFTER THE CHANGES OF MARCH 13

	Date	1		2		3		4	5
		12-hr. day		16-hr. day		24-hr. day		8-hr. day	4-hr. day
		A* Ht.	B* Ht.	A Ht.	B Ht.	A Ht.	B Ht.	Ht.	Ht.
I 20–24° C.	March 13	10.7		12.5		15.0		15.1	14.0
	April 5	11.7		14.4		17.7		16.2	15.5
	April 21	11.9		15.0		18.8		16.8	17.1
II 30–34° C.	March 13	14.0	22.7	16.9	19.7	21.1	18.5	10.7	10.2
	April 5	17.5	27.2	26.5	24.8	30.8	25.9	12.3	11.6
	April 21	19.4	29.7	30.8	26.7	34.0	28.3	13.8	13.8

* Previous to March 13 represented differences in moisture.

The appearance of the plants was very similar except that the plants of the longer day spread less in proportion to the height (pl. 46, fig. 2). The 24-hour-day plants at the higher temperature produced very few fruiting spikes, most of which were more like the ordinary vegetative branches. The plants at the lower temperature assumed a drooping appearance, whereas those at the higher temperature spread their leaves in the usual form. The plants at the lower temperature were more stocky. The total growth was practically twice as great at the higher temperature as at the lower temperature with the same length of day

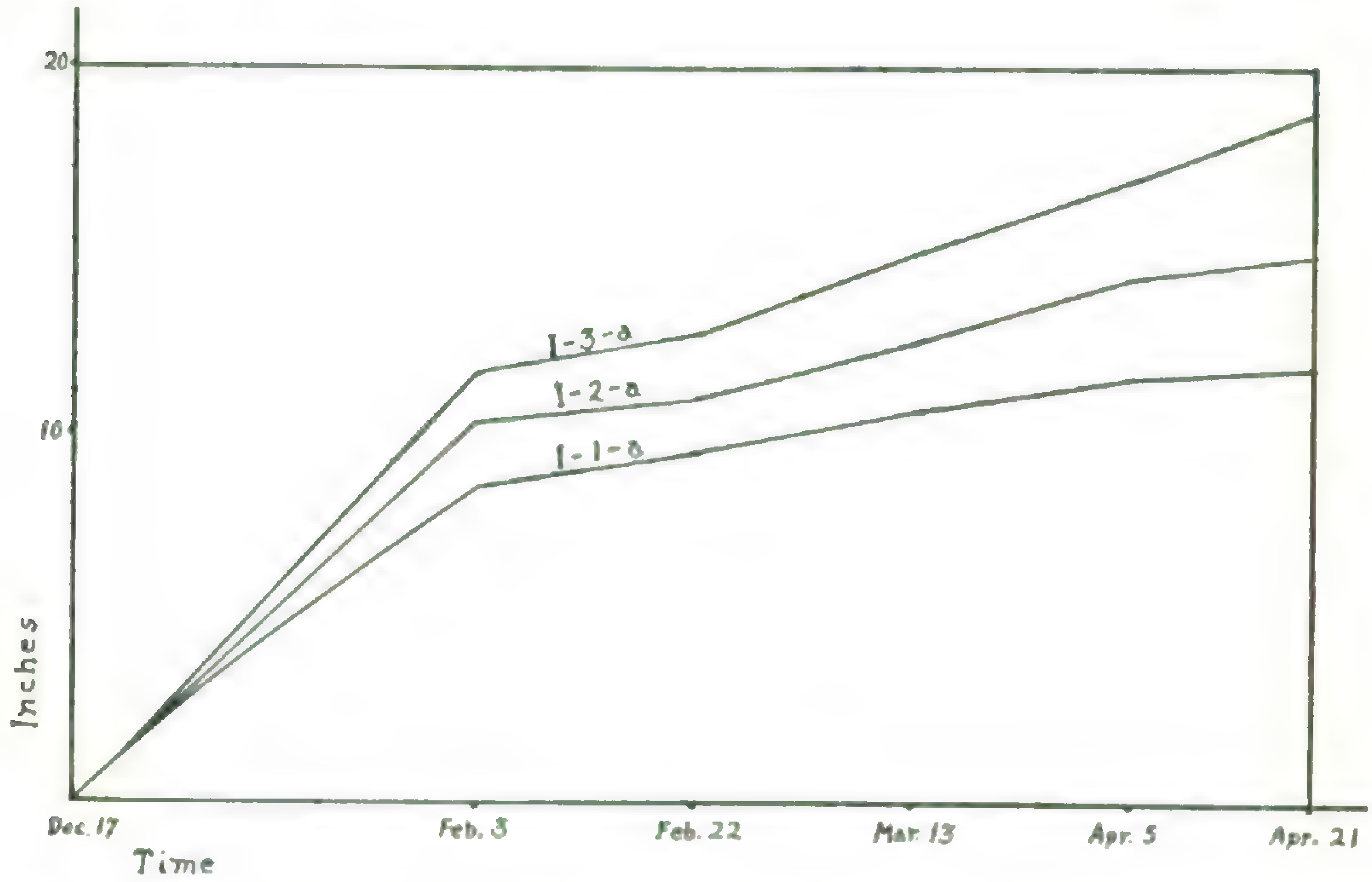


Fig. 2. The total growth in inches of the low-temperature plants plotted against the time. I-1-a, 12-hour-day plants; I-2-a, 16-hour-day plants; I-3-a, 24-hour-day plants.

(table III and pl. 46, fig. 3, and pl. 47). The growth rate was more regular at the lower temperature than at the higher temperature, giving a smoother growth curve. The difference in growth between the plants with higher and lower moistures was greater at the higher temperature (table III). Each division at the higher temperature showed considerably more growth with high moisture. The 12- and 16-hour-day plants at low temperature showed more growth with high moisture, whereas the 24-hour-day plants showed similar growth at high and low moistures (table III). The plants given less moisture shed more leaves than

those given the larger amount, especially those at the higher temperature.

The plants changed from a 12- to a 16-hour day showed a slight increase in growth rate for a few days, followed by a decline (fig. 4, section 1). Plants changed from a 12- to a 24-hour day

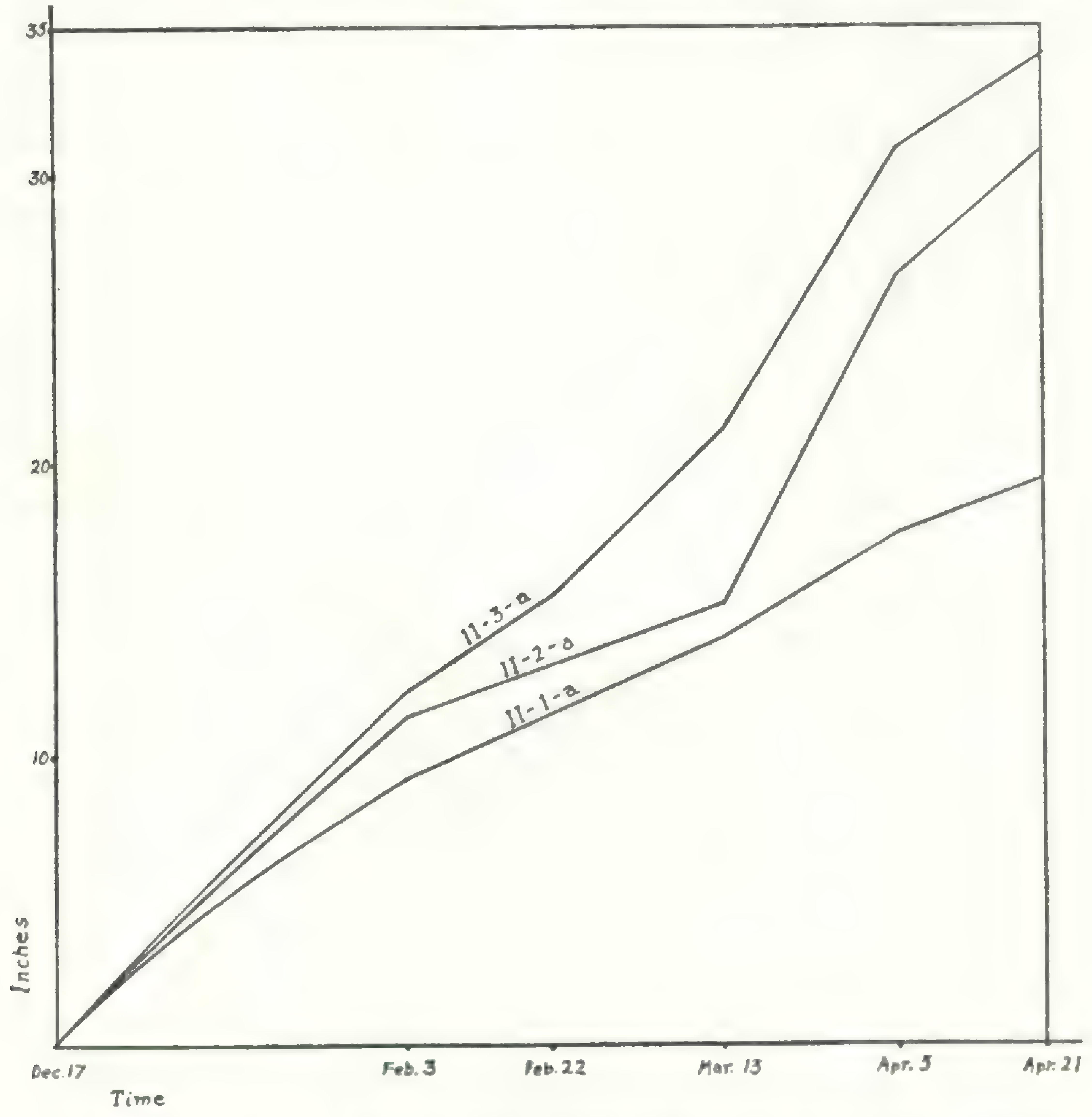


Fig. 3. The same as fig. 2 except the plants were grown at the higher temperature. II-1-a, 12-hour-day plants; II-2-a, 16-hour-day plants; II-3-a, 24-hour-day plants.

showed a marked increase in growth rate which was followed by an abrupt decline (fig. 4, section 1). Plants changed from a 16- to a 12-hour day showed a steady decline in growth for some time, followed by a very sudden increase accompanied by fruiting (fig. 4, section 2). Plants changed from a 16- to a 24-hour day showed an increase of growth rate followed by the usual decline (fig. 4, section 2). Plants changed from a 24- to 12- and 16-hour

days showed a steady decline in growth rate (fig. 4, section 3). The decline in growth rate after April 5 correlated with the usual decline of the cotton plant at this stage of development.

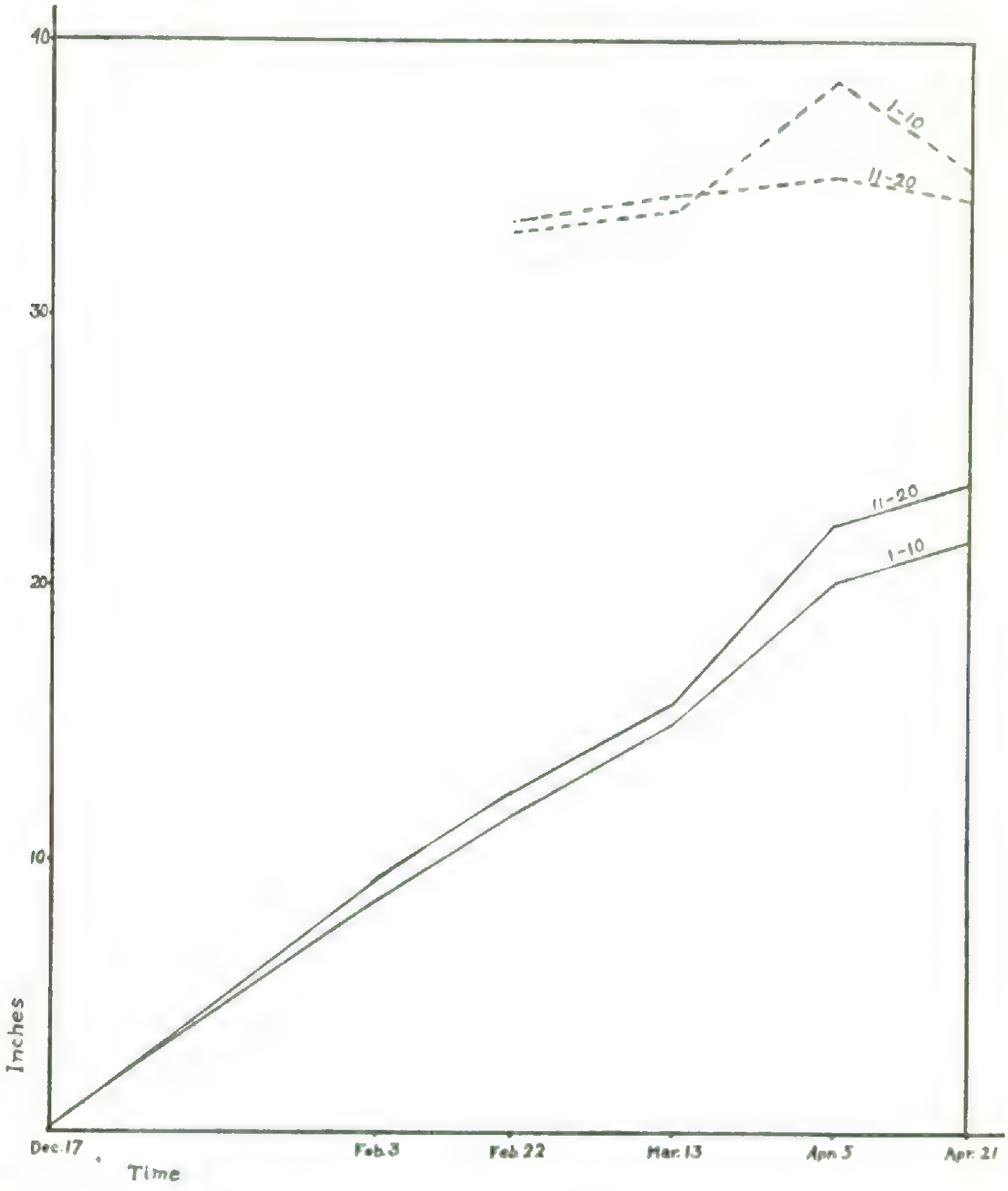


Fig. 4, section 1. The continuous lines represent the total growth in inches of the high-temperature plants changed from a 12- to 16- and 24-hour days plotted against the time. Plants 1–10 were changed from a 12- to a 16-hour day, whereas 11–20 were changed from a 12- to a 24-hour day.

The broken lines represent the growth per day of these plants plotted against the time. (Interchange numbers 1–10 and 11–20 in broken lines.) The growth rate is in hundredths.

Plants changed from 24- and 16-hour days to an 8-hour day showed a decline in growth rate. Those changed from a 12-hour

day to an 8-hour day showed an increase in growth rate. Groups of plants changed from the 12-, 16- and 24-hour days to a 4-hour day showed an increase in growth rate accompanied by chlorosis.

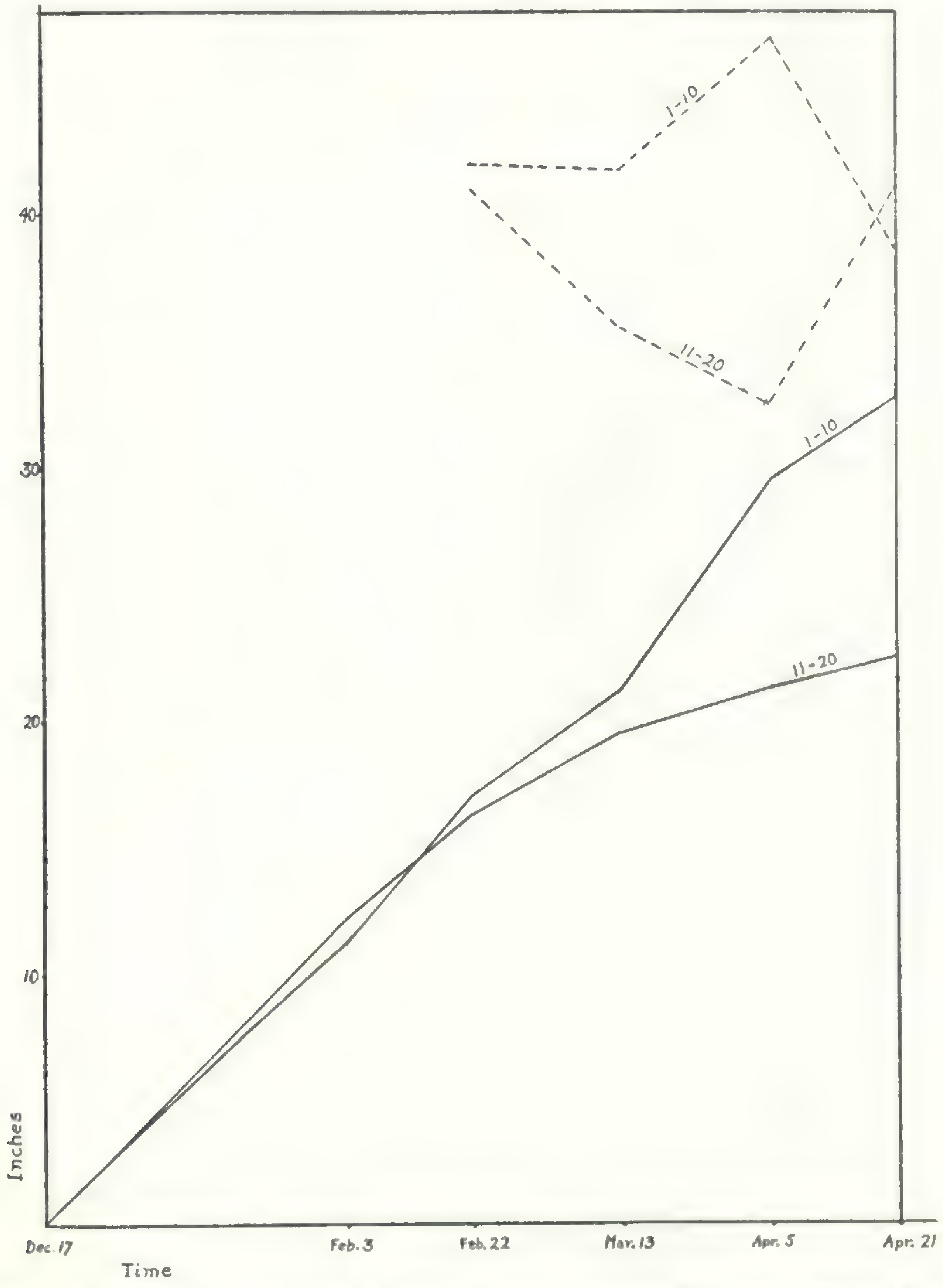


Fig. 4, section 2. The same as section 1, except plants 1–10 were changed from a 16- to a 24-hour day, and 11–20 from a 16- to a 12-hour day.

Experiment II.—As in experiment I, the amount of growth in height was proportional to the length of day at a given tempera-

ture (table v). At the same length of day the growth increased enormously with 9° C. difference in average temperature; the

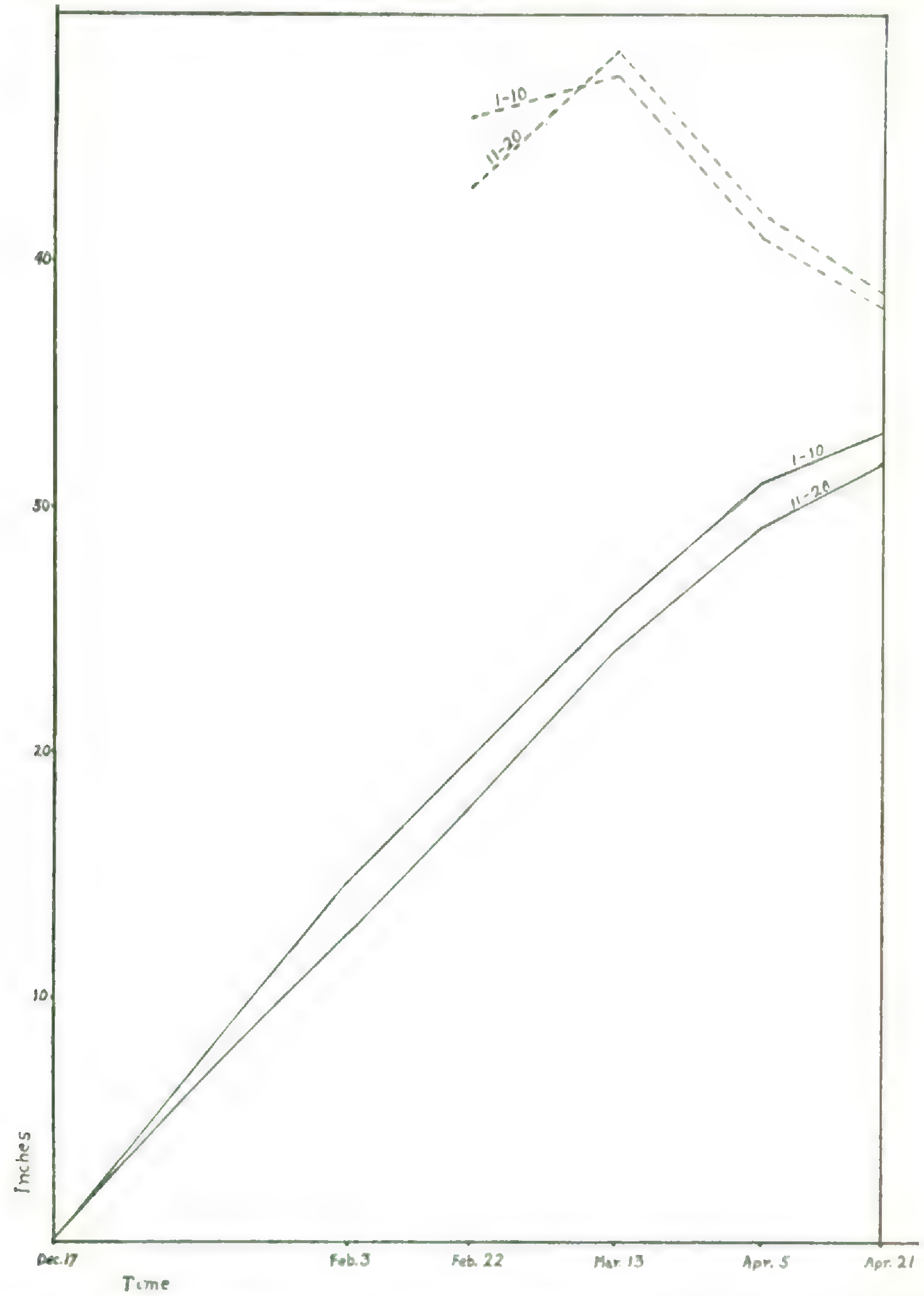


Fig. 4, section 3. The same as sections 1 and 2 except plants 1–10 were changed from a 24- to a 12-hour day, and 11–20 from a 24- to a 16-hour day.

plants grown at a higher temperature being more than twice as tall as those at a lower temperature and approximately twice as

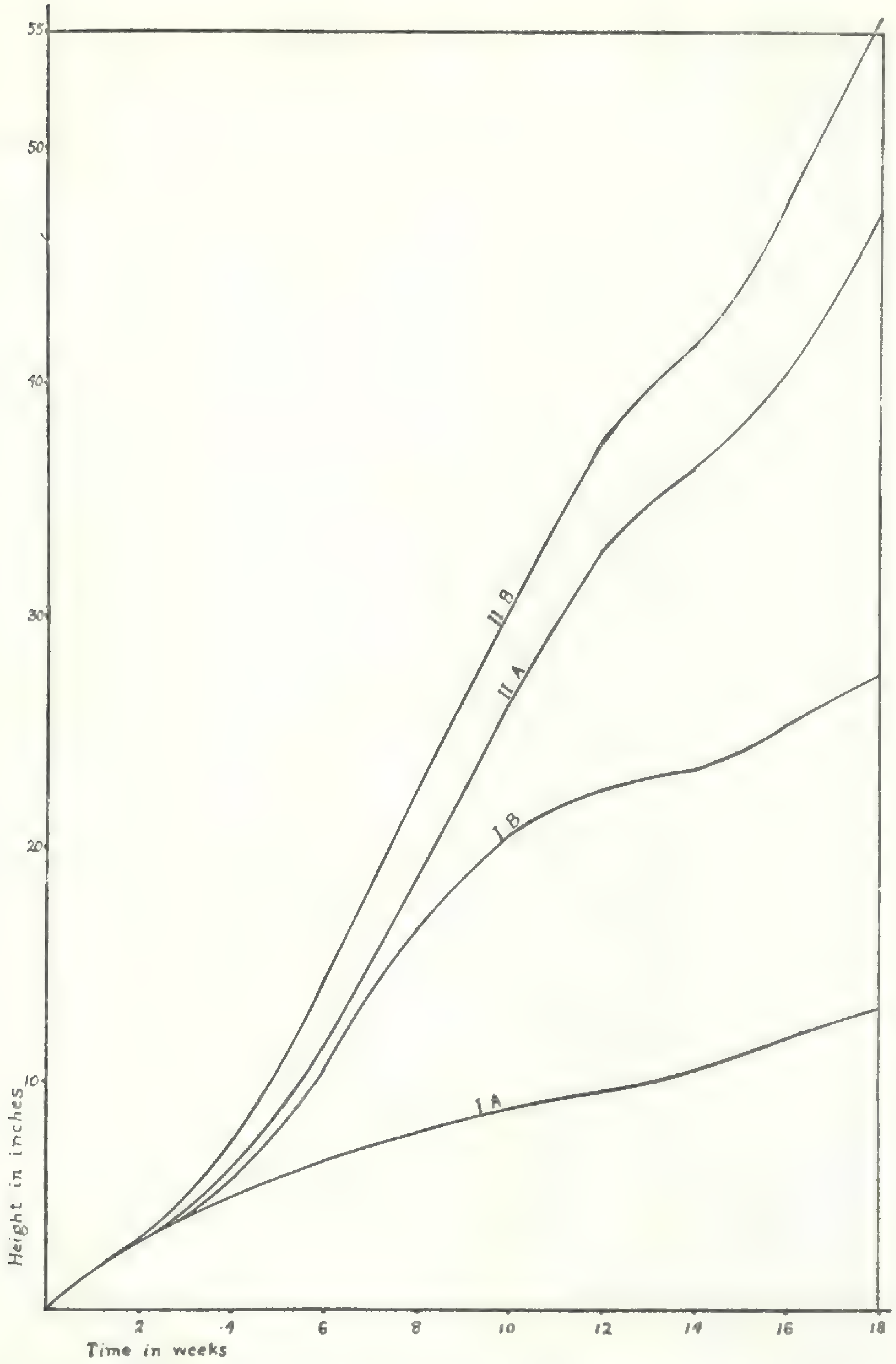


Fig. 5. Curves showing the growth in height of the respective sets; IA, lower temperature-short day plants, IB, lower temperature-long day plants, IIA, higher temperature-short day plants, and IIB, higher temperature-long day plants, as plotted in inches against the time in weeks.

heavy, both in green and in dry weight (tables v and vi, and fig. 5). The plants of the long day and higher temperature were slightly more succulent than those of the lower temperature; however, it will be noticed that the long-day plants of the lower temperature

TABLE V

THE AVERAGE HEIGHT IN INCHES OF EACH SET OF 50 PLANTS TAKEN ON THE RESPECTIVE DATES

	IA	IB	IIA	IIB
	Short day, low temp.	Long day, low temp.	Short day, high temp.	Long day, high temp.
Oct. 25	3.2	3.1	3.4	3.3
Nov. 8	4.2	5.7	6.2	7.4
Nov. 22	6.6	10.8	11.6	14.1
Dec. 6	7.9	16.5	18.9	22.4
Dec. 20	8.9	20.6	26.2	30.1
Jan. 3	9.6	22.5	32.8	37.5
Jan. 17	10.4	23.4	36.2	41.6
Jan. 31	11.9	25.3	40.5	48.0
Feb. 14	13.1	27.5	47.3	55.7

TABLE VI

STATISTICS OF THE SQUARES, LEAVES, INTERNODES, BRANCHES, AND GREEN AND DRY WEIGHTS PER PLANT TAKEN AT THE END OF EXPERIMENT II

	IA	IB	IIA	IIB
	Short day, low temp.	Long day, low temp.	Short day, high temp.	Long day, high temp.
Squares present	5.8	1.5	3.1	
Squares shed	1.2		.2	
Leaves present	16.9	9.5	18.3	19.4
Leaves shed	6.2	12.6	4.7	4.8
Internodes	18.	21.	23.	23.
Branches	6.1	1.9	.9	.3
Green weight	16.90	24.09	37.75	42.54
Dry weight	3.14	4.34	6.92	7.75

lost a large percentage of their leaves which affected both their green and dry weights (table vi). As shown by the growth curves (fig. 5) the growth rate was relatively low and approximately the same in all sets for the first two weeks. This is no doubt due to

the similar conditions of the early growth of the plants. The growth rate of the plants of the short day and lower temperature did not increase materially whereas that of the plants of a longer day and especially those of the higher temperature showed a gradual increase which reached a maximum after about three to four weeks (fig. 5). About 95 days after planting, all four sets showed a decrease in growth rate. At this time squares were developing on the lower temperature-short day plants and were noticed some days later on the lower temperature-long day plants and the higher temperature-short day plants, but no squares at all developed on the higher temperature-long day plants. A decrease in growth rate has been found to occur at about the age of flowering under normal conditions of the cotton belt, in both Experiments I and II, regardless of whether the plants were developing fruits or not. In Experiment II this decrease in growth rate was accompanied by a longer natural day which also gave light of greater intensity and an increase in temperature in both rooms (fig. 1). It is evident, therefore, that the decrease in growth rate was not due to poorer growing conditions but more probably to a natural decline during the period of reproduction. This decrease in growth rate was followed later by an increase as the days became longer and the light of greater intensity, even though the temperature was kept somewhat lower.

Except for height the general contour of the plants at a given temperature was the same regardless of the length of day. The lower-temperature plants developed larger leaves, shorter internodes, and in general were more stocky. The higher-temperature plants were more slender, with smaller leaves, longer internodes, and approached the appearance of a vine. It was necessary to stake up the higher-temperature plants. The lower-temperature plants developed an average of 18 and 21 internodes respectively, as compared with an average of 23 in the higher-temperature plants (table VI). The average length of the internodes on the lower temperature-short day plants was 0.72 inches, lower temperature-long day plants 1.28 inches, higher temperature-short day plants 2.05 inches, and higher temperature-long day plants 2.42 inches.

No fruiting branches developed on the higher temperature-long

day plants and few vegetative branches (table VI). The branches developed were for the most part on plants whose growing point had been injured, in which case one branch became dominant, taking the place of the main stem. Few fruiting branches of any size had developed on the higher temperature-short day plants and the lower temperature-long day plants, but a great number were observed in the early stages of development. The lower temperature-short day plants developed a number of fruiting branches and a few vegetative branches.

THE DEVELOPMENT OF FRUITS

Experiment I.—The appearance of squares varied considerably with the difference in length of day as well as with a difference in temperature. The first squares were noticed February 18 on the 12-hour-day plants in both the low- and the high-temperature sets. The plants receiving more moisture were the first to show a tendency to fruit but the difference was of little significance. The 16-hour-day plants produced at about the same time a few minute squares which were shed immediately, and no permanent squares appeared on the low-temperature plants until the first of March. The 16-hour-day plants at the high temperature shed the squares as rapidly as they appeared until near the middle of April; therefore, there were very few of any size when the experiment was concluded. The 24-hour-day plants at the low temperature developed permanent squares the first of March. The high-temperature plants with the exception of one individual did not develop permanent squares. The one exceptional plant produced one square which flowered on April 22, but it did not appear until after the temperature was allowed to go down below 25° C., due to a lack of heat in the greenhouse.

The first flowers appeared on the 12-hour-day plants at the high temperature on March 13. A number of flowers appeared in rapid succession until one or more bolls were set on each plant, after which a great number of the existing squares was shed either before or after flowering and new ones ceased to develop. The low-temperature plants did not produce flowers until April 1 after which time many flowers appeared in rapid succession and few squares and no bolls were shed before April 21. The first

flowers appeared on the 16-hour-day plants in the low-temperature group on April 4. Fewer flowers appeared on the 16-hour-day plants but bolls were set and grew very rapidly. No flowers appeared on the 16-hour-day plants at the high temperature. The first flower opened on the plants exposed to a 24-hour-day and low temperature April 21, but a number were opening and fruits were set within the next three days (pl. 46, fig. 1a).

Plants changed from a 12- to a 16-hour day continued to produce squares and to set fruits. The plants changed from a 12- to a 24-hour day did not produce so many flowers and in some cases abscissed all squares present, failing to set fruits at all. The fruits set were for the most part smaller and on longer branches than those of the 12- or the 16-hour-day plants.

TABLE VII

THE NUMBER OF SQUARES PER PLANT AND THE PER CENT SHED FROM THE TIME THE FIRST SQUARES APPEARED UNTIL MARCH 13

		1		2		3	
		12-hr. day		16-hr. day		24-hr. day	
		A Low Moist.	B High Moist.	A Low Moist.	B High Moist.	A Low Moist.	B High Moist.
I 20–24° C.	Sq. per plant	1.65	1.15	1.05	.95	.25	
	Sq. shed per plant	.1	.75	.25	.95	.1	.15
	Total forms per plant	1.75	1.9	1.3	1.9	.35	.15
	Per cent sq. shed	5.77	39.4	19.2	52.77	28.57	100.0
II 30–34° C.	Sq. per plant	2.45	2.55	.15	.15		
	Sq. shed per plant	.9	.95	.2	.35		
	Total forms per plant	3.35	3.5	.35	.5		
	Per cent sq. shed	26.85	27.14	57.14	70.0		

Plants changed from a 16- to a 12-hour day did not produce squares until March 26, but they flowered immediately thereafter, and soon all plants bore rapidly growing squares and a number bore fruits. Plants changed from a 16- to a 24-hour day, contrary to the general rule, produced squares as early as March 21. In a large number of plants all the squares were shed but in a few cases flowers opened and fruits were set. The plants setting

fruits were among those showing the highest growth rate at the time.

TABLE VIII

STATISTICS OF THE SQUARES, FLOWERS, AND BOLLS PER PLANT, AND OF ALL FORMS SHED THROUGHOUT THE EXPERIMENT. THE POSITIONS OF THE PLANTS ARE SHOWN AS THEY EXISTED FROM MARCH 13 TO APRIL 21

		1		2		3		4	5
		12-hr. day		16-hr. day		24-hr. day		8-hr. day	4-hr. day
		A*	B*	A	B	A	B		
I 20–24° C.	Sq. per plant	2.2		1.75		2.35		2.1	
	Fl. per plant	.25		.15					
	Bolls per plant	1.35		.8					
	Sq. shed per plant	2.85		2.85		1.55		1.7	1.5
	Total forms per plant	6.65		5.55		3.65		3.8	1.5
	Per cent sq. shed	42.85		51.35		39.74		44.15	100.0
II 30–34° C.	Sq. per plant	1.7	2.45	2.5	.65	.15	.4	2.3	
	Fl. per plant	.2							
	Bolls per plant	1.7	.15		.55		.51		
	Sq. shed per plant	5.65	.15	1.6	3.4	.45	4.55	1.6	1.4
	Fl. shed per plant	.1							
	Bolls shed per plant	.75			.65		.55		
	Total forms per plant	10.1	2.75	4.1	5.25	.6	6.01	3.9	1.4
	Per cent sq. shed	55.94	5.45	39.02	64.76	75.0	75.7	41.02	100.0
	Per cent flowers shed	3.77							
	Per cent bolls shed	27.65			54.16		51.88		

* Previous to March 13 represented differences in moisture.

The plants changed from a 24- to a 12-hour day developed squares, beginning April 8. No flowers opened before the experiment closed. Those changed from a 24- to a 16-hour day did not develop normal squares before the experiment was closed.

One or two vestigial squares appearing on one plant were immediately shed.

All squares present on the plants changed from the 12-, 16-, and 24-hour day to a 4- and 8-hour day were immediately shed. The 4-hour-day plants did not produce more squares. The 8-hour-day plants produced a second set of squares which grew very slowly and often showed a tendency to spread their bracts long before they were large enough to open. No flowers appeared. The results were due no doubt to the combination of a change in temperature and a change in the length of day.

Table VII shows the number of squares on each plant, the number shed, and the percentage of all squares shed up until March 13. Table VIII shows the number of squares, flowers and bolls per plant, and the percentage of each shed by the end of the experiment. The position of the plants is shown after the changes of March 13, but the individual calculations were made from the beginning until the experiment was closed April 21.

Experiment II.—The first squares were noticed on the lower temperature-short day plants on January 2. They developed slowly and did not open until near the middle of February. Squares were observed on the lower temperature-long day plants and higher temperature-short day plants the first week in February. No flowers were produced but some squares on the short day-higher temperature plants grew very rapidly and were showing signs of opening by February 14. No squares were developed on the higher temperature-long day plants.

When the plants were harvested on February 14 a single plant from the long day-higher temperature plants, which was of unusual height, was set to one side and kept growing under ordinary greenhouse conditions. The first squares were observed on May 15, and measurements at this time showed that the plant had grown only two inches in the last three months as compared with 76 inches in the four months under the higher temperature-longer day conditions.

Discussion

Much emphasis has been placed on relative day length as one of the most important factors in the natural environment of the plant. Not until recently has much attention been given to the

periodic responses of plants grown under various day lengths, as affected by variations in temperature. Due to the great complexity of environmental combinations, it is reasonable to assume that no one factor is responsible for a given response under all conditions. Temperature is recognized as a limiting factor in the zonation of plants, as well as in the process of photosynthesis (Blackman, '05). It has been shown by Gilbert ('26b) that temperature variations are important in the time of development of flower primordia and may be as effective as different day lengths, on some plants. Cotton is very sensitive to temperature changes as shown by Fung ('11), and therefore it is reasonable to expect that temperature would greatly modify the effects of the different lengths of day on the development of fruits and the percentage of fruits matured, as well as the vegetative growth. Similarly, under different combinations of factors, moisture or intensity of light might play the same role.

Gilbert suggests that under suitable environmental combinations specific temperatures may be found to substitute for relative day lengths in the development of flower primordia. This seems to be the case with the cotton plant. What determines the initiation of flower primordia is not known. Loew ('27) states that these responses are dependent on the presence of certain quantities of phosphoric acid as well as certain concentrations of the simple sugars in the cell sap. Gilbert ('26b) found under both low- and high-temperature conditions that the ratios of total carbohydrates to total nitrogen, and soluble carbohydrates to soluble nitrogen, were distinctly ascending as flower primordia are formed. What relation temperature changes and day length have on the formation of the necessary concentrations of these constituents is not known, but it is evident that flowering will take place under different combinations of conditions.

Sudden changes in the day length during the flowering period of the plant showed somewhat different results, and it was impossible with the small amount of data to determine when the flowering was initiated. It is possible that the flowering primordia are initiated but suppressed in their development under such conditions as higher temperature and long day, and when changed to a shorter day are allowed to develop, though somewhat slowly.

On the other hand, when the length of day is increased, the development is more rapid. Plants grown under a 4-hour day do not appear to be able to initiate flowering. It would seem that a very low percentage of carbohydrates would develop in plants under these conditions.

Branetzky ('97) observed that plants grow more slowly by day than by night. Balls, Lloyd, and others found that the cotton plant not only grows more slowly by day but that it shrinks a little during the hot part of the day. The shrinking is no doubt due to the loss of water by the rapidly transpiring cells under the temperature and humidity conditions of the noon-day sun. The cells in the region of the growing point are very elastic and will vary in size with the water content. This may limit the size of the cells maturing at this time, as the mature cell is more rigid and tends to plasmolyze instead of shrink with the loss of water. It is evident, however, that light has an effect on the development of the plant other than that of photosynthesis as shown by Went ('25, '28). The elongation and expansion of the cell wall are somewhat dependent on its stretching, due to turgidity. The nature of the stimulus of light on limiting this expansion is not known, but it appears to be other than the reduction of the water content. This stimulus appears to vary with the intensity of the light but no accurate measurements have been made under carefully controlled conditions. The limiting effects may be a direct relation of the absorption of the light rays by the protoplasm or an interrelation of the moisture and temperature of the cell as affected by the absorption of the light energy. Shortening the length of day as well as decreasing the intensity of the sunlight will affect the size and contour of the cells and the development of the leaves, stems and roots, as shown by Johannson ('27) and Doroshenko ('27). Since thicker leaves are produced by bright sunlight one would be led to believe that the sun has a direct influence other than temperature changes.

It is very difficult to determine at what length of day the light is more efficient per hour of illumination. If we judge by the elongation of the plant we must remember that plants tend to elongate more in proportion under lights of lower intensities, becoming extremely spindling if kept in the dark. If we choose

the development of fruits as a criterion we find that this does not necessarily correlate with the greatest vegetative growth. Lubimenko and Szeglova ('28) found that light was more efficient during an 8-hour day on cotton plants as measured by vegetative growth. In these experiments the greatest efficiency as measured by elongation was found to be at the long day, but as measured by dry weight, at the short day. This is evidenced by the more stocky appearance of the short-day plants (pl. 46, fig. 3) and the greater number of leaves per unit length (table VI). It must be borne in mind that the short-day plants are exposed to the light during the part of the day when the natural light is at its maximum intensity. It is probable that the more intense light of the noon-day is above the optimum for photosynthesis, but it has been shown by Johannson ('27) that light of this intensity stimulates the development of thicker leaves and a more stocky plant. On the other hand, the electric light is no doubt below the optimum for greatest efficiency in the production of photosynthates. It is evident, however, that these responses are greatly modified by differences in temperature and moisture (pl. 46, fig. 1 as compared with fig. 2).

Summary

1. Two experiments in successive years were made on the effects of the variations in temperature, moisture, and length of day, on the growth and reproduction of cotton.

2. In experiment I, cotton plants were grown in 4–5-inch pots under a 12-, 16- and 24-hour day, with variations in moisture and temperature. In experiment II, cotton plants were grown in 9-inch pots under a 12- and 20-hour day with a variation in temperature.

3. In experiment I a number of plants was changed from one length of day to another during the fruiting period.

4. The growth in height increased with the increase in length of day and was more than twice as great at the higher temperature.

5. All the plants grown at the lower temperatures produced squares, and in most cases set fruits regardless of the length of day. The short-day plants at higher temperature produced squares and set fruits. The long day-higher temperature plants, with the exception of one individual, did not produce squares.

6. Plants changed to a shorter day showed a decrease in growth rate followed in some cases by an increase after a few weeks. Plants changed to a longer day showed an increase in growth rate followed by a decline.

7. In most instances the growth rate declined during the fruiting season. Plants that did not produce fruits showed a similar decline in growth rate.

8. The plants changed to a longer day produced flowers and fruits in a short time. Plants changed from a 16- and 24-hour day to a 12-hour day produced squares and some set fruits after a few weeks. Plants changed from 12-, 16- and 24-hour days to an 8-hour day shed all squares present but developed new ones after some weeks. Plants changed from a 24- to a 16-hour day and from 12-, 16- and 24-hour days to a 4-hour day did not produce normal squares before the experiment closed.

9. Although the cotton plant may produce fruits more readily with a specific day length, thus being classed as a medium-day plant, one is led to believe from the above data that temperature differences may be substituted for day lengths in certain combinations. Fruiting may occur in the cotton plant under any given day length of 8 hours or above, providing the temperature and other factors are favorably adjusted.

The author wishes to express his gratitude to Dr. E. S. Reynolds of the Henry Shaw School of Botany, Washington University, for the numerous suggestions and criticisms during the progress of this work, and to Dr. G. T. Moore, Director of the Botanical Garden, for the use of the library of the Missouri Botanical Garden.

Bibliography

Adams, J. ('20). Relation of flax to varying amounts of light. Bot. Gaz. **70**: 153–156. 1920.

————, ('24 a). The effect on tomatoes, soy beans and other plants of altering the daily period of light. Am. Jour. Bot. **11**: 229–232. 1924.

————, ('24 b). Duration of light and growth. Ann. Bot. **38**: 509–523. 1924.

————, ('25). Some further experiments on the relation of light to growth. Am. Jour. Bot. **12**: 398–412. 1925.

Aso, K., and Umejiro, M. ('24). An experiment on the promotion of plant growth by the influence of electric light. [Japanese] Jour. Sci. Agr. Soc. 254: 31–36. *4 f.* 1924.

Atkinson, G. F. ('92). Some diseases of cotton. Ala. Agr. Exp. Sta. Bull. 41: 1–65. 1892. [Reprinted in the Bull. U. S. Dept. Agr. 33. 1896.]

Balls, W. L. ('12). The cotton plant in Egypt. Macmillan and Co., 1912.

Blackman, F. F. ('05). Optima and limiting factors. Ann. Bot. **19**: 281–295. 1905.

Branetzky, J. ('97). Die tägliche Periodizitat im Langenwachstum der Stengel. Acad. Imp. Sci. St. Petersburg, Mem. VII. **27**: 1–19. 1897.

Coit, J. E., and Hodgson, R. W. ('18). The June drop of Washington navel oranges. Calif. Agr. Exp. Sta., Bull. 290: 203–212. 1918.

Deats, Marian E. ('25). The effect on plants of the increase and decrease of the period of illumination over that of the normal day period. Am. Jour. Bot. **12**: 384–392. *2 pl.* 1925.

Detjen, L. R. ('26). Physiological dropping of fruits. Dela. Agr. Exp. Sta. Bull. 143: 5–47. 1926.

Doroshenko, A. ('27). Photoperiodism of some cultivated forms in connection with their origin. Bull. Appl. Bot. and Plant. Breed. **17**: 167–220. 1927.

Dutt, C. P. ('28). Abscission in cotton flowers. Bot. Gaz. **85**: 208–220. 1928.

Eaton, F. M. ('24). Assimilation-respiration balance as related to length of day reactions of soy beans. *Ibid.* **77**: 311–321. *f. 1–4.* 1924.

Eaton, S. V. ('31). Effects of variation in day length and clipping of plants on nodule development and growth of soy beans. Bot. Gaz. **91**: 113–143. 1931.

Fung, H. K. ('11). An ecological study of the American cotton plant with incidental reference to its possible adaptability in China. An unpublished doctor's thesis of Cornell University. June, 1911.

Garner, W. W., and Allard, H. A. ('20). Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. Jour. Agr. Res. **18**: 553–606. *pl. 64–79. 35 f.* 1920.

———, ———, ('27). Effect of short alternating periods of light and darkness on plant growth. Science N. S. **66**: 40–42. 1927.

———, ———, ('30). Photoperiodic response of soy beans in relation to temperature and other environmental factors. Jour. Agr. Res. **41**: 719–735. 1930.

———, ———, ('31). Effects of abnormally long and short alternations of light and darkness on growth and development of plants. *Ibid.* **42**: 629–652. 1931.

Gilbert, B. E. ('26 a). The response of certain photoperiodic plants to differing temperature and humidity conditions. Ann. Bot. **40**: 315–320. 1926.

———, ('26 b). Interrelation of relative day length and temperature. Bot. Gaz. **81**: 1–24. 1926.

Harvey, R. B. ('22 a). Growth of plants in artificial light. *Ibid.* **74**: 447–451. *f. 1–2.* 1922.

———, ('22 b). Growth of plants in artificial light from seed to seed. Science N. S. **56**: 366–367. 1922.

Johansson, N. ('27). Einige Versuche über die Einwirkung verschiedener Belichtung auf die vegetative Entwicklung von *Raphanus sativus* L. Flora **121**: 222–235. *7 f.* 1927.

Kellerman, K. F. ('26). A review of the discovery of photoperiodism: The influence of the length of daily light periods upon the growth of plants. Quart. Rev. Biol. **1**: 87–94. *pl. 1–8.* 1926.

Koningsberger, V. J. ('23). Lichtintensität und Lichtempfindlichkeit. Rec. Trav. Bot. Néerland. **20**: 257–312. *f. 1–10.* 1923.

Lloyd, F. E. ('16). The abscission of flower-buds and fruits in Gossypium and its relation to environmental changes. Roy. Soc. Canada, Trans. **10** Sect. IV: 55–61. 1916.

————, ('20 a). Abscission of fruits in *Juglans californica quercina*. *Ibid.* Sect. V. **14:** 17–22. *f. 1–5.* 1920.

————, ('20 b). Environmental changes and their effects upon boll-shedding in cotton. N. Y. Acad. Sci., Ann. **29:** 1–131. 1920.

Loew, O. ('27). Was gibt den Anstoss zur Bluten bildung? Fortschr. Landwirthschaft. **2:** 105–106. 1927.

Lubimenko, V. N., et Szeglova, O. A. ('28). L'adaptationa photoperiodique des plantes. Rev. Gén. Bot. (Paris) **40:** 513–536. *f. 1–3.* 1928.

Martin, R. D., and Loomis, H. F. ('23). Summer irrigation of pima cotton. Jour. Agr. Res. **23:** 927–946. 1923.

Mason, T. G. ('22 a). Growth and abscission in sea island cotton. West Indian Bull. **19:** 214–238. 1922.

————, ('22 b). Growth and abscission in sea island cotton. Ann. Bot. **36:** 457–484. 1922.

McClelland, T. B. ('24). The photoperiodism of *Tephrosia candida*. Jour. Agr. Res. **28:** 445–460. 1924.

Munerati, O. ('24). Illuminazione artificiale notturna come mezzo per accelerare le fasi del ciclo dei vegetali. Atti. R. Accad. Naz. Lincei Roma (Rendiconti Cl. Sci. Fis. Mat. e Nat.) **33:** 402–405. 1924.

Namikawa, I. ('26). Contributions to the knowledge of abscission and exfoliation of floral organs. Imp. Univ. Sapporo Japan, Jour. Coll. Agr. Hokkaido. **17:** 63–131. 1926.

Redington, G. ('30). A study of the effect of diurnal periodicity upon plant growth. Roy. Soc. Edinburgh, Trans. **56:** part II no. 12. 1930.

Sorauer, P. ('22). Manual of plant diseases. [Trans. by Frances Dorrance.] 1922.

Tinker, M. A. ('24). Effect of length of day on flowering and growth. Nature **114:** 350–351. *2 f.* 1924.

Tjebbes, J. C., and Uphof, Th. ('21). Der Einfluss des Elektrische Lichtes auf das Pflanzenwachstum. Landw. Jahrb. **56:** 315–328. *10 f.* 1921.

Toole, E. H., and Drummond, P. L. ('24). The germination of cotton seed. Jour. Agr. Res. **28:** 285–292. 1924.

Wanser, H. M. ('22). Photoperiodism of wheat: a determining factor in acclimatization. Science N. S. **56:** 313–315. 1922.

Went, F. W. ('25). Concerning the difference in sensibility of the tip and base of Avena to light. K. Akad. Wet. Amsterdam, Proc. **29:** 1–7. 1925.

————, ('29). Wuchsstoff und Wachstum. Rec. Trav. Bot. Néerl. **25:** 1–116. *f. 1–13.* 1929.

Zimmerman, P. W., and Hitchcock, A. E. ('29). Root formation and flowering of dahlia cuttings when subjected to different day lengths. Bot. Gaz. **87:** 1–13. *6 f.* 1929.

Explanation of Plate

PLATE 46

Fig. 1. Showing the effects of the difference in the length of day on the growth of cotton at low temperature; *a*, bolls. Two plants at the extreme right, 12-hour-day plants; two in the center, 16-hour-day plants; two at the extreme left, 24-hour-day plants.

Fig. 2. Showing the effects of the difference in the length of day on the growth of cotton at high temperature. Two plants at the extreme right, 12-hour-day plants; two in the center, 16-hour-day plants; two at the extreme left, 24-hour-day plants.

Fig. 3. Showing the effects of different temperatures on the growth of 12-hour-day plants.

1

2

3

BERKLEY—EFFECTS OF DIFFERENT LENGTHS OF DAY AND TEMPERATURES

Explanation of Plate

PLATE 47

Fig. 1. Showing the effects of different temperatures on 16-hour-day plants. Two plants at the extreme right, low-temperature plants; two at the left, high-temperature plants.

Fig. 2. Showing the effects of different temperatures on 24-hour-day plants. Two plants at the right, low-temperature plants; two at the left, high-temperature plants.

1

2

BERKLEY—EFFECTS OF DIFFERENT LENGTHS OF DAY AND TEMPERATURES

GENERAL INDEX TO VOLUME XVIII

New scientific names of plants and the final members of new combinations are printed in **bold face** type; synonyms, and page numbers having reference to figures and plates, in *italics;* and previously published names and all other matter, in ordinary type

A

abietinus (Polystictus), 470
Abietis (Trametes), 474
Acidity of Missouri soils and its relation to plant distribution, A study of, 41
Adansonia, 128
adustus (Polyporus), 471
Agaricaceae, 470
Agaricus boletiformis, 391; *hirsutus*, 391; *saepiarius*, 391; *trabeus*, 392
Aleurodiscus disciformis, 485; **diffissus,** 485
Allium stellatum, Chromosome complements of, 465, *468;* Moly, 465; ursinum, 465
Alpova, a new genus of Rhizopogonaceae, with further notes on Leucogaster and Arcangeliella, 457
Alpova cinnamomeus, 461, *464*
Althaea, 118, 125
ambiens (Helicoma), 10
ammonis (*Gyroceras*), 1, 7
ammonis (Sarcopodium) (Tricholeconium), 7
amorphus (Polyporus), 471
anastomosans (Helicoma), 13, 14, *16*
Anderson, Edgar. The chromosome complements of Allium stellatum and Nothoscordum bivalve, 465; and Dorothea De Winton. The genetic analysis of an unusual relationship between self-sterility and self-fertility in Nicotiana, 97
Anechites adglutinata, 552
Anisolobus cognatus, 546; *Perrottetii*, 546
Antrodia mollis, 367
Apocynaceae of tropical America, New or otherwise noteworthy, 541
applicatus (Pleurotus), 470
Arcangeliella **australiensis,** 463; **Ravenelii,** 463; **rosea,** 462; **Stephensii,** 463
Arenaria cephaloidea, 284
arida (Coniophora), 485
Asclepiadaceae, New South American, 557
Asia, eastern, Hymenomycetous fungi of, 469
Aurantiporellus alboluteus, 333
auricula-Judae (Auricularia), 487
Auricularia auricula-Judae, 487; auriformis, 487
Auriculariaceae, 487
auriformis (Auricularia), 487
auriscalpium (Hydnum), 477
australiense (Hydnangium), 463
australiensis (Arcangeliella), 463
australiensis (*Octaviana*), 463

B

Bacteria, effect of ultra-violet radiation on, 18, 505
badio-ferruginea (Hymenochaete), 483
Beardsley, Martha L. The cytology of Funaria flavicans Michx. with special reference to fertilization, 509
bellus (Helicomyces), 10, 16
benzoinus (Polyporus), 471
Berkley, Earl E. Studies of the effects of different lengths of day, with variations in temperature, on vegetative growth and reproduction in cotton, 573
bicolor (Odontia), 479
biformis (Polystictus), 471
Bjerkandera adusta, 339, 340
Blepharodon **minimus,** 557; suberectus, 557
Boletus abietinus, 328; *adustus* 339, var. *crispus*, 340; *albidus*, 337; *applanatus*, 374; *arcularius*, 346, 394; *benzoinus*, 338; *caesius*, 337; *calceolus*, 358; *carpineus*, 339; *cinnabarinus*, 342; *cinnamomeus*, 354; *coccineus*, 342; *conchatus*, 384; *confluens*, 352, 353; *coriaceus*, 353; *crispus*, 340; *elegans*, 359; *ferruginosus*, 401; *fuliginosus*, 338; *fulvus*, 377, 383; *fuscoporus*, 339; *hirsutus*, 324; *igniarius*, 382; *incarnatus*, 328; *incertus*, 397; *isabellinus*, 339; *lipsiensis*, 374; *marginatus*, 377; *medulla-panis*, 398; *nigromarginatus*, 324; *nummularis*, 359; *odoratus*, 370; *ovinus*, 350; *pelleporus*, 339; *perennis*, 353; *Pini*, 379; *pinicola*, 377; *pomaceus*, 383; *resinosus*, 338; *Rheades*, 336; *roseus*, 387; *salicinus*, 384; *semiovatus*, 377; *sistotremoides*, 347; *spumeus*, 345; *squamosus*, 356; *suberosus flabelliformis*, 339; *subtomentosus*, 353; *ungulatus*, 377; *varius*, 358; *versicolor*, 323
brisbanense (*Hydnangium*), 463
brumalis (Polyporus), 471
Bucholtz, Alexander F. The effect of monochromatic ultra-violet light of

measured intensities on behavior of plant cells, 489
Burt, Edward Angus. Hymenomycetous fungi of Siberia and eastern Asia—mostly of wood-destroying species, 469
byssoidea (Coniophora), 485

C

caesio-alba (Poria), 476
calcea (Sebacina), 487
Calcium content of higher plants, effect of ultra-violet radiation on, 565
Callirhoë, 125; *spicata*, 159, 165
Calyptospora columnaris, 293
Cantharellus alveolaris, 394
Capnorea pumila, 286
Card, H. H. A revision of the genus Frasera, 245
Carestianum (Septobasidium), 487
Celtidis f. *fulvescens* (*Gyroceras*), 4
Celtidis (*Gyroceras*), 2, 3
Celtidis (Helicoceras), 3, *8*
Celtidis (*Monilia*), 3
Chailletii (Stereum), 480
Chromosome complements of Allium stellatum and Nothoscordum bivalve, 465
cinnamomeus (Alpova), 461, *464*
citrinus (Leucogaster), 462
Cladomeris Schweinitzii, 347
Clarksville soils in Missouri, 48
Clavaria formosa, 486
Clavariaceae, 486
colliculosum (*Corticium*), 484
Colorado: The Polyporaceae of, 287; zones of vegetation in, 289
Coltricia cinnamomea, 354; *connata*, 353; *perennis*, 353; *tomentosa*, 349
commune (Schizophyllum), 470
confluens, (Corticium), 483
conformis (Ditiola), 486
confragosa (Daedalea), 475
Coniophora arida, 485; byssoidea, 485; olivacea, 485; **sibirica,** 485
Coremiella saxonicum, 7
Coriolellus Sepium, 366; *serialis*, 365
Coriolus abietinus, 328; *hexagoniformis*, 366; *hirsutulus*, 323; *Lloydii*, 326; *nigromarginatus*, 324; *pargamenus*, 330; *planellus*, 344; *prolificans*, 330; *subchartaceus*, 331; *versicolor*, 323; *zonatus*, 325
cornucopioides (Craterellus), 479
corticalis (Peniophora), 484
Corticium *colliculosum*, 484; confluens, 483; frustulosum, 483; galactinum, 483; hydnans, 484; illaqueatum, 484; investiens, 484; lactescens, 484; laeve, 484; ochraceum, 484; polygonium, 484; radiosum, 484; roseum, 484; sulphureum, 484
Cotton, Studies of the effects of different lengths of day, with variations in temperature, on vegetative growth and reproduction in, 573
Craterellus cornucopioides, 479
Cryptoporus volvatus, 321
Cucumbers, effect of ultra-violet radiation: on growth, 27, 30, 568; on calcium content, 570; on phosphorus content, 569
Curtisii (Helicoma), 10
Cyanide, effect of, on cultures of Fusarium lini, 75
Cyclomyces, 314
Cytidia salicina, 486
Cytokinesis in the Mosses, 533
Cytology of Funaria flavicans Michx. with special reference to fertilization, 509, *536*, *538*, *540*

D

Dacryomycetaceae, 486
Dacryomyces abietinus, 292
Daedalea, 314, 376; aurea, 476; confragosa, 475; *epigaea*, 347; *heteromorpha*, 366; *mollis*, 367; *Pini*, 379; quercina, 476; *saepiaria*, 391; *trabea*, 392; unicolor, 476, var. *violacea*, 328
Dasyscypha Agassizii, 292; arida, 292
Day, effects of different lengths of, with variations in temperature, on vegetative growth and reproduction in cotton, 573
delectans (Polyporus), 472
De Winton, Dorothea, Edgar Anderson and. The genetic analysis of an unusual relationship between self-sterility and self-fertility in Nicotiana, 97
dichrous (Polyporus), 472
diffissa (*Peniophora*), 485
diffissus (Aleurodiscus), 485
Dipladenia **Achrestogyne,** 543; congesta, 544; fragrans, 545; glabra, 545; Martiana, 545; **oblongifolia,** 544; surinamensis, 545; **upatae,** 545; urophylla, 545
disciformis (Aleurodiscus), 485
Distribution of some Rocky Mountain plants, 283
Ditiola conformis, 486
Dodecatheon tetrandrum, 284
Dodge, C. W. **Alpova,** a new genus of Rhizopogonaceae, with further notes on Leucogaster and Arcangeliella, 457
dryadeus (Polyporus), 472

E

Echites *agglutinata*, 552; *circinalis*, 552; *coalita*, 552; *cognata*, 546; *Dusenii*,

552; *portobellensis*, 553; *Sanctae-Martae*, 555; *spectabilis*, 552
Eichleriella spinulosa, 487
Elfvingia applanata, 374; *lipsiensis*, 374; *megaloma*, 374
ellipticum (Helicoon), 11
Elytropus spectabilis, 552
Erinaceus (Hydnum), 477
Exidia glandulosa, 292, 487
Exolobus **marmoreus**, 561; patens, 562

F

Farlowii (Podaxis), 459, *464*
fasciatum (Stereum), 480
Favolus, 394; alveolaris, 394, *454*; *canadensis*, 394; *europaeus*, 394; *ohiensis*, 394; *striatulus*, 394
Femsjonia luteo-alba, 487
Fertilization: in Funaria flavicans Michx., 509, *536*, *538*, *540*; in the Mosses, 509; in the Liverworts, 511
fibrillosus (Polyporus), 472
Flax, glucoside content of, 66
floccosus (Leucogaster), 459
Fomes, 376; *Abietis*, 379; *alboluteus*, 333; annosus, 389, *450*; *applanatus*, 374; conchatus, 384; connatus, 396; Demidoffii, 385, 388, *446*; *Earlei*, 385; *Ellisianus*, 388; fraxinophilus, 389, f. Ellisianus, 388, *452*; *fuliginosus*, 338; fulvus, 383, *446*, 474; igniarius, 382, *448*, 474; *Juniperinus*, 385; *leucophaeus*, 374; *marginatus*, 377; *megaloma*, 374; *nigricans*, 382; nigrolimitatus, 380, *454*; ohiensis, 376; Palliseri, 474; Pini, 379, *442*; pinicola, 377, *444*, *446*, 474; *pomaceus*, 383; *ponderosus*, 378; putearius, 381; roseus, 372, 387, *436*, 474; scutellatus, 376; *tenuis*, 363; *ungulatus*, 377
Fomitopsis *annosa*, 389; *pinicola*, 377; *rosea*, 387
formosa (Clavaria), 486
Fossombronia, fertilization in, 512, 530
Frasera, A revision of the genus, 245
Frasera, 256; *albicaulis*, 269, f. *alba*, 269; albomarginata, 274, *280*, var. **induta**, 275; *ampla*, 259; *angustifolia*, 259; *carolinensis*, 262; caroliniensis, 262, *280*; coerulea, 271; *Cusickii*, 270; fastigiata, 264, *280*; *induta*, 275; *macrophylla*, 259; montana, 266, *280*; neglecta, 265, *280*; nitida, 267, *280*, var. **albicaulis**, 269, *280*, var. **Cusickii**, 270, *280*, *282*; *nitida* var. *albida*, 267; *officinalis*, 262; paniculata, 275, *280*; Parryi, 273, *280*; puberulenta, 272, *280*, *282*; speciosa, 258, *280*; *speciosa* var. *angustifolia*, 259, var. *scabra*, 259, var. *stenosepala*, 259; *stenosepala*, 259; *thyrsiflora*, 264; tubulosa, 271, *280*; *utahensis*, 275; *venosa*, 259; *verticillata*, 262; *Walteri*, 262
Friesii (Porothelium), 476
frondosus (Polyporus), 472
frustulosum (Corticium), 483
Fuller, Harry J. Stimulatory effects of radiation from a quartz mercury vapor arc upon higher plants, 17; F. Lyle Wynd and. Some effects of ultra-violet radiation upon the calcium and phosphorus content of higher plants, 565
Fulvifomes Juniperinus, 385
fulvus (Fomes), 474
Funalia stuppea, 368
Funaria flavicans Michx., cytology of, 509; hygrometrica, 512
Fusarium lini, 66
fuscopes (Helicomyces), 15
Fuscoporia ferruginosa, 401
fusco-violaceus (Irpex), 478
fuscum (Stereum), 481

G

galactinum (Corticium), 483
Ganoderma, 373; applanatum, 374, *442*; *leucophaeum*, 374; *lipsiensis*, 374
Gasteromycetes, 457
gausapatum (Stereum), 481
Genetic analysis of an unusual relationship between self-sterility and self-fertility on Nicotiana, 97
gibbosa (Trametes), 475
gigantea (Peniophora), 485
gilvus (Polyporus), 472
glabrum (Hydnangium), 463
glandulosa (Exidia), 487
Gloeophyllum abietinellum, 391; *hirsutum*, 370, 391; *pallidofulvum*, 393; *trabeum*, 393
Glucoside content of flax, 66
Goodman, George J. Notes on the distribution of some Rocky Mountain plants, 283
griseum (Helicosporium), 9
Guepinia monticola, 292
Gyroceras, 1; *ammonis*, 1, 7; *Celtidis*, 2, 3, f. *fulvescens*, 4; *divergens*, 4; *Nymphaearum*, 5; *Plantaginis*, 5; *saxonicum*, 7
Gyrocerus, 2

H

Haemadictyon circinalis, 552
Hagerstown soils in Missouri, 44
Helicoceras, The genus, 1
Helicoceras, 1; **Celtidis**, 3, *8*; **Nymphaearum**, 5, *8*; **Oryzae**, 2, 6, *8*; **Plantaginis**, 5, *8*
Helicoma ambiens, 10; **anastomosans**, 13, 14, *16*; Curtisii, 10; Morgani, 13, 14; olivaceum, 11; polysporum, 11; repens,

11; **tenuifilum,** 14, *16;* violaceum, 14; **Westoni,** 12, *16*
Helicomyces bellus, 10, 16; **fuscopes,** 15; roseus, 10, 16
Helicoon ellipticum, 11
Helicosporeae, Brief notes on the, with descriptions of four new species, 9
Helicosporium griseum, 9; lumbricoides, 10; lumbricopsis, 10; *Nymphaearum,* 5; phragmites, 9
Hesperalcea, 137, 214; *malachroides,* 128, 215
Hesperochiron pumilus, 284
Heterobasidion annosum, 389
heteromorpha (Lenzites), 470
Hexagona, 394; *alveolaris,* 394; *micropora,* 394; *Mori,* 394; *striatula,* 394
hirsutum (Stereum), 481
hirsutus (Polystictus), 471
hispida (Trametes), 474
hispidus (Polyporus), 472
Hollii (Hydnum), 477
Host plants for species of Polyporaceae, 294
Hydnaceae, 477
Hydnangium australiense, 463; *brisbanense,* 463; *glabrum,* 463; *nudum,* 462; *Ravenelii,* 463; *Stephensii,* 463, v. *Ravenelii,* 463; *virescens,* 462
hydnans (Corticium), 484
Hydnum auriscalpium, 477; Erinaceus, 477; Hollii, 477; **Murashkinskyi,** 477; ochraceum, 478; **reflexum,** 478; velutinum, 478
Hydrocyanic acid in flax, 66
Hymenochaete badio-ferruginea, 483; Mougeotii, 483; tabacina, 483
Hymenomycetous fungi of Siberia and eastern Asia—mostly of wood-destroying species, 469
Hypochnus spongiosus, 480; umbrinus, 480
Hysterangium, 457

I

igniarius (Fomes), 474
illaqueatum (Corticium), 484
inodora (Trametes), 474
Inonotus dryophilus, 336; *fibrillosus,* 334
investiens (Corticium), 484
Irpex, 334; fusco-violaceus, 478; *grossus,* 368; lacteus, 478; pachyodon, 479
Ischnoderma fuliginosum, 338; *resinosum,* 338

J

Juglandis (Microstroma), 486

K

Kneiffia setigera, 479

L

lacteus (Irpex), 478
lacteus (Polyporus), 473
lactescens (Corticium), 484
laevigata (Poria), 476
laricina (Lenzites), 470
Laubertia Boissieri, 556; **Pringlei,** 555; **Sanctae-Martae,** 555
laeve (Corticium), 484
lentus (Polyporus), 473
Lenzites, 390; abietina, 392; *abietinella,* 391, *452; abietis,* 328; heteromorpha, 470; *heteromorpha,* 366, 470; laricina, 470; *rhabarbarina,* 391; saepiaria, 391, *452; saepiaria porosa,* 370; septentrionalis, 470; serpens, 315; tenuis, 470; trabea, 392, *454; vialis,* 392
Lesquerella Kingii, 284; prostrata, 284
Leucocraspedum, 257; *albicaule,* 269; *albomarginatum,* 274; *coeruleum,* 271; *montanum,* 266
Leucogaster, 457; citrinus, 462; floccosus, 459; *luteomaculatus,* 462; nudus, 462
Light: effect of, on glucoside content of flax, 73; effect of, on growth and reproduction in plants, 573; ultra-violet, effect of measured intensities on behavior of plant cells, 489
Linamarine, 90
Linder, D. H. The genus Helicoceras, 1; Brief notes on the Helicosporeae, with descriptions of four new species, 9
Linkage between self-sterility allelomorphs and other genes, 108
Liverworts, fertilization in, 511
lumbricoides (Helicosporium), 10
lumbricopsis (Helicosporium), 10
luteo-alba (Femsjonia), 487
luteomaculatus (*Leucogaster*), 462

M

Macropharynx *fistulosa,* 552; **spectabilis,** 552
Macroscepis barbata, 560; **equatorialis,** 559
Malouetia **Killipii,** 551; pubescens, 552
Malva, 125; *malachroides,* 215, 217
Malvaceae, 124
Malvastrum 128; *confertum,* 213; spicatum, 128
Mandevilla, 556
Marsdenia **lauretiana,** 562; mollissima, 563
Melanogaster, 457
melanopus (Polyporus), 473
Mertensia incongruens, 286
Merulius, 322; *alveolaris,* 394; serpens, 477; tremellosus, 477
Mesadenia, 246, 257
Microstroma Juglandis, 486

Missouri soils, acidity of, 41
Mnium: effect of ultra-violet radiation on cell contents of leaves, 500; fertilization in, 510
Moisture: influence of, upon spore germination and growth, 300; soil, effect of, on growth of cotton plants, 578
Monilia Celtidis (Celtis), 2
Monilia Celtidis, 2, 3
Monochromatic ultra-violet light of measured intensities, Effect of, on behavior of plant cells, 489
Monochromator in ultra-violet radiation work, 496
Morgani (Helicoma), 13, 14
Mosses, fertilization in, 509
mucida (Poria), 476
Murashkinsky, K. E. Fungi received from, 469
Murashkinskyi (Hydnum), 477
Mougeotii (Hymenochaete), 483
mutata (Peniophora), 485
Myriadoporus adustus, 339

N

Nicotiana, self-sterility and self-fertility in, 97
Nicotiana alata, 97, × Langsdorfii, 97; Sanderae, 97
Nothoscordum bivalve, Chromosome complements of, 465
nudum (*Hydnangium*), 462
nudus (Leucogaster), 462
Nuttallia malvaeflora, 188
Nymphaearum (*Gyroceras*), 5
Nymphaearum (Helicoceras), 5, *8*
Nymphaearum (*Helicosporium*), 5

O

ochraceum (Corticium), 484
ochraceum (Hydnum), 478
ochroleucum (Stereum), 469, 481
Ochroporus odoratus, 370
Octaviania australiensis, 463; *Ravenelii*, 463; *rosea*, 462; *Stephensii*, 463, v. *Ravenelii*, 463
Octavianina Stephensii, 463
Odontadenia **affinis,** 549; **augusta,** 548; **cognata,** 546; coriacea, 551; Cururu, 549; geminata, 551; **glauca,** 550; hypoglauca, 551; **Killipii,** 546; nitida, 551; **Perrottetii,** 546; **polyneura,** 546, 551; **Sandwithiana,** 547; speciosa, 548; **stemmadeniaefolia,** 548
Odontia bicolor, 479
olivacea (Coniophora), 485
olivaceum (Helicoma), 11
Oryzae (Helicoceras), 6, *8*
osseus (Polyporus), 473

P

pachyodon (Irpex), 479
Palliseri (Fomes), 474
palmata (Thelephora), 479
Paramecia, effect of ultra-violet radiation on, 505
Paxina nigrella, 293
Pellia, fertilization in, 512, 530
Pelloporus perennis, 353
Peniophora corticalis, 484; *diffissa*, 485; gigantea, 485; mutata, 485; *quercina*, 484
pergamenus (Polystictus), 471
Phaeoporus applanatus, 374
Phaeolis sistotremoides, 347
Phaeostemma grandifolia, 561; **tigrina,** 560
Phellinus igniarius, 382; *isabellinus*, 363; *nigrolimitatus*, 380; *salicinus*, 384
Phellorinia, 459
Phlebia radiata, 479; strigoso-zonata, 479
Phosphorus content of higher plants, effect of ultra-violet radiation on, 565
phragmites (Helicosporium), 9
Physiology of plant disease, Studies in the, 57
Pini (Stereum), 482
pinicola (Fomes), 474
Placodes applanatus, 374; *fulvus*, 383; *pomaceus*, 383
Plantaginis (*Gyroceras*), 5
Plantaginis (Helicoceras), 5, *8*
plantaginis (Torula), 5
Pleurococcus, effect of ultra-violet radiation on cell contents of, 499
Pleurotus applicatus, 470
Podaxis, 459; anomalus, 459; Farlowii, 459, *464*
polygonium (Corticium), 484
Polyporaceae, 470; of Colorado, 287; factors determining the distribution of, 296
Polyporus, 317; abietinus, 328, *414;* adustus, 339, *420*, 471; alboluteus, 333, *416;* amorphus, 471; anceps, 343, *424; annosus*, 389; *applanatus*, 374; *arculariformis*, 346; arcularius, 346, *426; aurantiacus*, 334; benzoinus, 471; *benzoinus*, 338; borealis, 335, *418; Boucheanus peponinus*, 394; brumalis, 471; caesius, 337, *434; calceolus*, 358; *callosus*, 365; *caudicinus*, 356; *cervinus*, 367; cinnabarinus, 342, *426;* cinnamomeus, 354, *426;* circinatus, 349, *430; circumstans*, 388; *conchatus*, 384; confluens, 351, *434; corruscans*, 336; crispus, 340, *424;* cryptopus, 355, *428;* delectans, 472; *Demidoffii*, 385; dichrous, 472; dryadeus, 472; *dryophilus*, 336; *dualis*, 349; elegans, 359, *432;*

Ellisianus, 343; *ferruginosus*, 401; fibrillosus, 316, 334, *412*, 472; *Flabellum*, 329; fragilis, 341, *426*; frondosus, 472; *fuliginosus*, 338; *fulvus*, 338; *Gillotii*, 389; gilvus, 472; *hirsutulus*, 323; hirsutus, 324, *412*; hirtus, 357, *432*; *hispidellus*, 357; *hispidoides*, 347; hispidus, 472; *hyperboreus*, 382; *igniarius*, 382; *ilicincola*, 330; *inflatus*, 321; *irregularis*, 389; *Juniperinus*, 385; *laceratus*, 329; lacteus, 473; *laetificus*, 400; lentus, 473; leucomelas, 288; *leucophaeus*, 374; leucospongia, 326, *412*; *Lindheimeri*, 368; *Lloydii*, 326; *loricatus*, 384; *Macouni*, 401; *marginatus*, 377; *medulla-panis*, 398; *megaloma*, 374; melanopus, 473; *Menandianus*, 329; mollis, 342; *nigricans*, 382; *nigrolimitatus*, 380; *Novae-Angliae*, 382; *oblectans*, 354; *obvolutus*, 321; *odoratus*, 370; osseus, 360, 473; ovinus, 350, *426*; *pallescens*, 339; pargamenus, 329, *410*; *parvulus*, 328, 354; *Peakensis*, 349; perennis, 353, *430*; *piceinus*, 379; picipes, 359; *Pini*, 379; *pinicola*, 377; planellus, 344, *422*; *planus*, 344; *pomaceus*, 383; *prolificans*, 329; *pseudopargamenus*, 330; pubescens, 326; *purpurea*, 401; resinosus, 338, 389, *422*, 473; Rheades, 336, *420*; *roseus*, 387; *rufo-pallidus*, 387; *salicinus*, 384; *salmonicolor*, 400; *Sartwellii*, 330; *scalaris*, 365; Schweinitzii, 347, *428*; *serialis*, 365; *serpentarius*, 389; *Shiraianus*, 334; *spectabilis*, 347; *spissus*, 400; splendens, 354; spumeus, 345, *434*, 473; squamosus, 356, 473; *steroides*, 367; *subacida*, 399; subchartaceus, 331, *414*; *subcinereus*, 339; *subflavus*, 330; *subpileatus*, 389; *subsericeus*, 354; subsquamosus, 356; *tabulaeformis*, 347; *tenuis*, 363; *tomentosus*, 349; trichrous, 473; *ursinus*, 332, *416*; *vaporaria*, 397; *variiformis*, 365; varius, 358, *432*; versicolor, 323, *410*; volvatus, 321, *410*; *volvatus Helix*, 321; *xalapensis*, 330; *xantholoma*, 398; *Zelleri*, 360; zonatus, 325, *410*
polysporum (Helicoma), 11
Polystictus, 313; *abietinus*, 328, 470; *azureus*, 323; *biformis*, 471; *Celottianus*, 368; *cinnabarinus*, 342; *cinnamomeus*, 354; *Fergussoni*, 368; *hirsutus*, 324, 471; *hirtellus*, 324; *pargamenus*, (*pergamenus*), 330; *perennis*, 353; pergamenus, 471; *piceinus*, 379; *pusio*, 328; radiatus, 471; *Schweinitzii*, 347; *scuirinus*, 368; *subchartaceus*, 331; *versicolor*, 323; vulpinus, 471; *zonatus*, 326
Poria, 313, 395; caesio-alba, 476; *callosa*, 365, 396; contigua, 364; ferruginosa, 364, 401; *incerta*, 397; *laetifica*, 400; laevigata, 476; *Macouni*, 401; medullapanis, 398, *456*; monticola, 396, *454*; mucida, 398, 476; *obducens*, 396; purpurea, 401; *salmonicolor*, 400; spissa, 400, *456*; subacida, 399, *456*; superficialis, 364; taxicola, 476; Vaillantii, 398; vaporaria, 397, *456*; violacea, 401; viticola, 364; xantha, 476; *xantholoma*, 398
Porodaedalea Pini, 379
Porothelium Friesii, 476
Prestonia acutifolia, 554; **agglutinata,** 552; **coalita,** 552; **Dusenii,** 552; **isthmica,** 555; *Langlassei*, 555; *macrocarpa*, 553; mexicana, 555; Muelleri, 553; **portobellensis,** 553; Riedelii, 553; **velutina,** 554
protracta (Trametes), 475
pubescens (Polyporus), 473
Pycnoporellus fibrillosus, 334
Pycnoporus cinnabarinus, 342
Pyropolyporus conchatus, 384; *Earlei*, 385; *fulvus*, 383; *Juniperinus*, 385

Q

Quartz mercury vapor arc, Stimulatory effects of radiation from, 17
quercina (Daedalea), 476
quercina (*Peniophora*), 484
Quinhydrone electrode method for testing soils, 41

R

radiata (Phlebia), 479
radiata (Trametes), 475
Radiation: Stimulatory effects of, from a quartz mercury vapor arc, 17; ultraviolet, effect of, upon plants, 489, upon the calcium and phosphorus content of higher plants, 565
radiatus (Polystictus), 471
radiosum (Corticium), 484
Rauwolfia bahiensis, 543; **lauretiana,** 541; paucifolia, 542; **sanctorum,** 542
Ravenelii (Arcangeliella), 463
Ravenelii (*Hydnangium*), 463
Ravenelii (*Octaviania*), 463
reflexum (Hydnum), 478
repens (Helicoma), 11
resinosus (Polyporus), 473
Reynolds, Ernest S. Studies on the physiology of plant disease, 57
Rhabdadenia polyneura, 546
Rhaptocarpus coalitus, 552
Rhizopogon, 457
Rhoeo discolor, effects of ultra-violet radiation on cell contents of, 499
rhytidocyclum (Stereum), 482

Riccardia, fertilization in, 512, 530
Rocky Mountain plants, Notes on the distribution of some, 283
rosea (*Octaviania*), 462
rosea (Arcangeliella), 462
roseum (Corticium), 484
roseus (Fomes), 474
roseus (Helicomyces), 10, 16
Roush, Eva M. Fling. A monograph of the genus Sidalcea, 117
rugosiusculum (Stereum), 482
rugosum (Stereum), 482
rutilans (Polyporus), 473

S

salicina (Cytidia), 486
sanguinolentum (Stereum), 482
Sarcopodium, 2
Sarcopodium (Tricholeconium) **ammonis,** 7
saxonicum (Coremiella), 7
saxonicum (*Gyroceras*), 7
Schizophyllum commune, 470
Scutiger cryptopus, 355; *hispidellus*, 357; *laeticolor*, 352; *ovinus*, 350; *Whiteae*, 352
Sebacina calcea, 487
Self-sterility and self-fertility in Nicotiana, Genetic analysis of an unusual relationship between, 97
septentrionalis (Lenzites), 470
Septobasidium Carestianum, 487
serpens (Merulius), 477
Sesia hirsuta, 391; *pallidofulva*, 393
setigera (Kneiffia), 479
Shope, Paul Franklin. The Polyporaceae of Colorado, 287
Siberia, Hymenomycetous fungi of, 469
sibirica (Coniophora), 485
Sida, 117, 125, 197; *californica*, 199; *delphinifolia*, 143, 145, 188, 193, 197; *diploscypha*, 139, *heterophylla*, 173; *malvaeflora*, 175, 188; *oregana*, 168
Sidalcea, A monograph of the genus, 117
Sidalcea, 117, 136; sect. **Annuae,** 138; *asplenifolia*, 175, 177; asprella, 201; *atacosa*, 218; atropurpurea, 218; *californica*, 199; calycosa, 145, *230;* campestris, 175; *campestris*, 169, 218; candida, 153, *228, 234; candida* var. *tincta*, 153; *confinis*, 179; *Covillei*, 187; *crenulata*, 179; *Cusickii*, 174; *delphinifolia*, 188, var. *humilis*, 189; diploscypha, 139, *228, 232; diploscypha* var. *minor*, 139; *elegans*, 202; subgenus Eusidalcea, 129, 138; *eximia*, 159; *favosa*, 200; glaucescens, 207; Hartwegi, 148, *230; Hartwegi* var. *tenella*, 148; subgenus Hesperalcea, 128, 214; Hendersoni, 157; Hickmani, 212; Hickmani var. Parishii, 213, *228, 230, 244; Hickmani*, 213; hirsuta, 143, *230; humilis*, 188; *hydrophila*, 159; *interrupta*, 166; malachroides, 215, *228, 230, 244;* malvaeflora, 188, *228, 240*, var. atropurpurea, 218, var. californica, 199, var. Listeri, 218; *malvaeflora*, 157, 168, 179, var. *asprella*, 202, var. *Oregana*, 157, 168; subgenus **Malvastralcea,** 128, 212; mariana, 218; mexicana, 218; *montana*, 207; multifida, 209, *240; "Murrayana,"* 159; *Nelsoniana*, 159; neo-mexicana, 179, var. **Covillei,** 187, var. **parviflora,** 186; *neo-mexicana* var. *Diehlii*, 179; *nervata*, 169; *nitrophila*, 186; nodosa, 218; oregana, 168, 177, *230, 236*, var. **Cusickii,** 174; *oregana*, 175; *Parishii*, 213; *parviflora*, 186, var. *Thurberi*, 179; pedata, 210, *242;* sect. **Perennes,** 151; peruviana, 218; *ranunculacea*, 166; reptans, 200; *rhizomata*, 145; **robusta,** 205; *rostrata*, 189; *scabra*, 189; *secundiflora*, 139; spicata, 159, var. **ranunculacea,** 166, *230, 238; spicata* var. *pedata*, 210, var. *reptans*, 200; *sulcata*, 145; *sylvestris*, 175; *tenella*, 148; triloba, 218; *valida*, 159; virgata, 178; *vitifolia*, 215
Sidalcia, 145
Soils in Missouri, the acidity of, and its relation to plant distribution, 41
spadiceum (Stereum), 483
Sphaeralcea, 213; pedatifida, 218
Sphaerocarpos, fertilization in, 511, 530
spinulosa (Eichleriella), 487
Spongipellis borealis, 335; *fragilis*, 341; *occidentalis*, 345; *spumeus*, 345
spongiosus (Hypochnus), 480
Spongiporus leucospongia, 326
spumeus (Polyporus), 473
squamosus (Polyporus), 473
Stephanotella Glaziovii, 558; **Killipii,** 558
Stephensii (Arcangeliella), 463
Stephensii (*Hydnangium*), 463
Stephensii (*Octaviania*), 463
Stephensii v. *Ravenelii* (*Hydnangium*), 463
Stephensii (*Octavianina*), 463
stereoides (Trametes), 475
Stereum bicolor, 481; Chailletii, 480; fasciatum, 480; fuscum, 481; gausapatum, 481; hirsutum, 481; ochroleucum, 469, 481; Pini, 482; rhytidocyclum, 482; rugosiusculum, 482; rugisporum, 292; rugosum, 482; sanguinolentum, 482; spadiceum, 483; sulcatum, 483; versiforme, 483
Steyermark, Julian A. A study of plant distribution in relation to the acidity of various soils in Missouri, 41

Stimulatory effects of radiation from a quartz mercury vapor arc upon higher plants, 17
Streptotrachelus Pringlei, 555
Strilia cinnamomea, 354
Studies on the physiology of plant disease, 57
suaveolens (Trametes), 475
sulcatum (Stereum), 483
sulphureum (Corticium), 484
Sweertia, 257; *albicaulis*, 269; *albomarginata*, 274; *Bigelowii*, 279; *carolinensis*, 262; *fastigiata*, 264; *Parryi*, 273; *radiata*, 259
Swertia, 245, 247
Swertia, 257; *albomarginata*, 274; *difformis*, 262; *fastigiata*, 264; *Frasera*, 262; *neglecta*, 263; *nitida*, 265; *Parryi*, 273; *tubulosa*, 271

T

tabacina (Hymenochaete), 483
Tabernaemontana hirtula, 541; **Killipii**, 541
taxicola (Poria), 476
Temperature: effect of, on glucoside content of flax, 73; effect of variations in, and lengths of day, on vegetative growth and reproduction in cotton, 573; influence of, upon spore germination and growth, 297
tenuifilum (Helicoma), 14, *16*
tenuis (Lenzites), 470
tenuis (Thelephora), 479
terrestris (Thelephora), 480
Tessaranthium, 257; *angustifolium*, 259; *macrophyllum*, 259; *scabrum*, 259; *speciosum*, 259; *stenosepalum*, 259
Tesseranthium, 246, 257; *radiatum*, 259
Thelephora palmata, 479; **tenuis**, 479; terrestris, 480
Thelephoraceae, 479
Tilsit soils in Missouri, 42
Tomatoes, effect of ultra-violet radiation: on growth, 28, 36, 568; on calcium content, 570; on phosphorus content, 569
Torula Plantaginis, 5
Tradescantia reflexa, effect of ultra-violet radiation on cell contents of stamen hairs, 499
Trametes, 362; Abietis, 474; *benzoina*, 338; *carnea*, 372; *cinnabarina*, 342; gallica, 369; gibbosa, 475; heteromorpha, 366, *440;* hispida, 368, *440*, 474; inodora, 474; isabellina, 363, *438; laceratus*, 366; *mollis*, 367; odorata, 370, *440; Peckii*, 368; *Pini*, 379; *Pini Abietis*, 379; *protracta*, 370, 475; **radiata,** 475; *radiciperda*, 389; serialis, 365, *438; setosus*, 363; stereoides, 367, *440*, var. Kmetii, 475; stuppeus, 370; suaveolens, 475; subrosea, 372, *442; tenuis*, 363; *trabea*, 475; variiformis, 365, *438*
tremellosus (Merulius), 477
Tremellaceae, 487
Tricholeconium, 2
trichrous (Polyporus), 473
Tyromyces anceps, 343; *caesius*, 337; *Ellisianus*, 343

U

Ultra-violet light, Effect of monochromatic, of measured intensities, on behavior of plant cells, 489
Ultra-violet radiation: effects of, upon plants, 17, 489; Some effects of, upon calcium and phosphorus content of higher plants, 565
umbrinus (Hypochnus), 480
Ungulina annosa, 389; *fuliginosa*, 338; *marginata*, 377; *rosea*, 387; *volvata*, 321, var. *pleurostoma*, 321
unicolor (Daedalea), 476
Union soils in Missouri, 47

V

velutinum (Hydnum), 478
versiforme (Stereum), 483
Villarsia pumila, 286
violaceum (Helicoma), 14
virescens (*Hydnangium*), 462
Vita-glass filter in ultra-violet radiation experiments, 30
vulpinus (Polystictus), 471

W

Westoni (Helicoma), 12, *16*
Wherry's soil acidity results, compared with Steyermark's, 51
Woodson, Robert E. Jr. New or otherwise noteworthy Apocynaceae of tropical America, 541; New South American Asclepiadaceae, 557
Wynd, F. Lyle, and Harry J. Fuller. Some effects of ultra-violet radiation upon the calcium and phosphorus content of higher plants, 565

X

xantha (Poria), 476

Z

Zea Mays, effect of ultra-violet radiation on, 566

Annals
of the
Missouri Botanical Garden

A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Graduate Laboratory of the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

The Annals of the Missouri Botanical Garden appears four times during the calendar year: February, April, September, and November. Four numbers constitute a volume.

Subscription Price - - - $6.00 per volume
Single Numbers - - - - 1.50 each

Contents of previous issues of the Annals of the Missouri Botanical Garden are listed in the Agricultural Index, published by the H. W. Wilson Co.

STAFF
OF THE MISSOURI BOTANICAL GARDEN

Director,
George T. Moore.

Assistant to the Director,
Katherine H. Leigh.

Hermann von Schrenk,
Pathologist.

Jesse M. Greenman,
Curator of the Herbarium.

Edgar Anderson,
Geneticist.

Ernest S. Reynolds,
Physiologist.

David H. Linder,
Mycologist.

Anton Hogstad, Jr.,
Pharmacognosist.

Roland V. La Garde,
Research Assistant.

Robert E. Woodson, Jr.,
Research Assistant.

Nell C. Horner,
Librarian and Editor of Publications.

BOARD OF TRUSTEES
OF THE MISSOURI BOTANICAL GARDEN

President,
George C. Hitchcock.

Vice-President,
Samuel C. Davis.

Second Vice-President,
Daniel K. Catlin.

L. Ray Carter.
Thomas S. Maffitt.
George T. Moore.
Albert T. Perkins.
Philip C. Scanlan.
Ethan A. H. Shepley.
Fred G. Zeibig.

EX-OFFICIO MEMBERS:

George R. Throop,
Chancellor of Washington University.

Frederick F. Johnson,
Bishop of the Diocese of Missouri.

Victor J. Miller,
Mayor of the City of St. Louis.

A. F. Satterthwait,
President of The Academy of Science of St. Louis.

Emil J. Barth
President of the Board of Education of St. Louis.

Daniel Breck, *Secretary.*